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THE AMERICAN SPECIES OF SARCOSTEMMA R. BR. (ASCLEPIADACEAE)*

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As subjects for monographic study the Asclepiadaceae have been rather generally neglected since the beginnings of taxonomy. This may have been due, in part perhaps, to their minor economic importance and to the impression that genera in the family are easy neither to define nor to determine. A more important factor, however, has been the prevalent opinion that the flowers are so complex morphologically as to render the plants very difficult to study. One cannot deny with candor that these points are well-taken, but the result has been that no satisfactory general account of the family exists, making identification extremely arduous. Many ill-correlated small genera have been described because of their presumed uniqueness; and the vast potential of absorbing morphologic and ecologic topics in this interesting group has not been appreciated.

I was led to consider the Asclepiadaceae because of my interest in their adaptations for insect pollination and the bearing which this has on their phylogeny. It is remarkable that the pattern of evolution and the taxonomic difficulties encountered in this family and in the Orchidaceae are very similar. Except for certain differences which will be discussed below, these two families, the most specialized for insect pollination in Dicotyledones and Monocotyledones respectively, show similar developments in floral structure, aggregation of the pollen into pollinia, and a bewildering array of forms which almost defy classification. In many respects, however, the Asclepiadaceae are much the more specialized with regard to structure of the pollinium and the method of pollination. And their floral evolution, though to a certain extent parallel with that of the orchids, has been along slightly different lines. For example, the Asclepiadaceae are constructed upon a basic pattern of actinomorphy, in contrast to the strongly zygomorphic orchids. To what

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extent can we attribute these similarities and differences to the intimate relationship between the plants and their insect pollinators?

It soon became apparent that a study of these subjects can only be based on a dependable taxonomic system and a clear understanding of the morphology of the structures involved. With these points in mind, an investigation of *Sarcostemma* was undertaken as an introduction to the complexities of tropical American Asclepiadaceae. Not without a thorough review of all the genera, however, can the ideals of a sound morphology and taxonomy be realized, and it is not suggested that this account of one genus is more than an introduction to a program that would require years of study to complete.

Sarcostemma probably has been the least neglected of the genera in its alliance, for the plants are attractive both scientifically and esthetically. In the New World, the species are vines with umbelliform or racemiform inflorescences of fragrant, showy flowers. The flower, with the waxy corona bladders in the center, somewhat resembles that of the wax plant, *Hoya*, in those species with rotate corollas. The species of the group formerly assigned to *Philibertia*, which have campanulate flowers, were often cultivated in English greenhouses of the past century. And still fairly common in collections of succulents are the leafless African and Asian species, which occasionally produce clusters of yellow or green flowers.

In this paper, the New World species of *Sarcostemma* have been studied monographically; and, in order to maintain perspective, the Old World forms are treated synoptically. Unfortunately, the paucity of specimens and the general nomenclatural confusion of the Eastern Hemisphere species make it impossible to gain any understanding of their relationships, or even to estimate the number of species involved. It is possible that the evolutionary development of these species of the drier parts of the tropical and subtropical regions of the Old World has been along different lines from that of the New World forms. At any rate, many rather obscure genera are confused in the literature, and also, the misapplication of such names as *viminale* and *aphyllum* for leafless plants, throughout most of the Old World floristic accounts, has created a situation of extreme taxonomic chaos. A number of leafless species of *Euphorbia* have been confused with the sarcostemmas so that it is by no means easy to decide which family is being discussed in a given treatment.

With the detailed knowledge of the American species in mind, I have begun a reinvestigation of the morphology of the flower in the tribe Asclepiadeae. The results of such a study can be used as a basis for a classification of genera and species enabling one to view them as a whole and helping to remove that impression of chaos which has discouraged so many.

HISTORY OF THE GENUS

I do not propose to record in detail the history of the various species which have been attributed to *Sarcostemma* and its segregates. It seems desirable, however, to chronicle briefly those genera which have been related nomenclaturally. In order

to understand the taxonomic history of *Sarcostemma*, it is essential to recognize that there are two main problems involved. First, there is the misapplication of several generic names and the consequent confusion in their usage up to the present day. Second, there is the question of how many segregates can be maintained without endangering the integrity of the genus as a practical unit.

Sarcostemma was described by Robert Brown[1] in 1809 in his classic paper on the separation of the Apocynaceae and Asclepiadaceae. The only species known to him at that time were succulent lianas of Asia and Africa having the leaves reduced to scales. They were characterized by rotate flowers provided with a pronounced faucal annulus or outer corona, and an inner corona consisting of five separate, inflated lobes (to which the name alludes). Ten years later, Kunth[2] described, as species of *Sarcostemma*, a series of American forms of similar floral structure, but with laminate leaves. For a species having the corolla campanulate, he inaugurated the new genus *Philibertia* HBK. He also noted that the outer corona in *Philibertia* was less prominent than in *Sarcostemma*.

In his account of the Asclepiadaceae for the 'Prodromus' of De Candolle, Decaisne[3] recognized only the genus *Sarcostemma*, which consisted, however, of two sections: EUSARCOSTEMMA and PHILIBERTIA. The former included both New World and Old World forms with rotate corollas, while the latter contained only New World species with "*corolla urceolato-rotata*." Decaisne himself described most of the American species of both EUSARCOSTEMMA and PHILIBERTIA included in his account.

The peculiar confusion in the taxonomy of the genus began in 1876 when Bentham[4] referred all of the New World species to the genus *Philibertia* HBK., regardless of the shape of the corolla. Shortly thereafter, Gray[5] and Hemsley[6] made the necessary new combinations for species of the United States and Latin America. Fournier[7], on the other hand, in the 'Flora Brasiliensis', followed Decaisne in the use of *Sarcostemma* for rotate-flowered species, although he had to deal with no species of *Philibertia* (*sensu* HBK.).

In the preparation of his treatment of the Asclepiadaceae for Martius' great work, Fournier apparently made a careful study of the Latin American species. It is interesting to note that a tendency to draw taxonomic lines rather finely was emphasized in his establishment of the genera *Funastrum*[8] and *Cystostemma*[9]. Of the two species included within *Funastrum* by Fournier, only one is referable to *Sarcostemma*, this being *F. angustissimum* (Anderss.) Fourn. of the Galapagos Islands. The other is an Argentine species of *Cynanchum (Ditassa)*. *Cystostemma* was erected for a species which completely lacks the faucal annulus or ring of the corona; in all other respects it is so close to the other New World sarcostemmas

[1] R. Brown, in Mem. Wern. Soc. 1:50. 1809.
[2] Kunth, in HBK. Nov. Gen. et Sp. Pl. 3:195. 1819.
[3] Decaisne, in DC. Prodr. 8:537. 1844.
[4] Bentham, in Benth. & Hook. Gen. Pl. 2:733. 1876.
[5] Gray, in Proc. Amer. Acad. 12:64–65. 1877.
[6] Hemsley, in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:320. 1881.
[7] Fournier, in Mart. Fl. Brasil. 6[4]:233–235. 1885.
[8] Fournier, in Ann. Sci. Nat. Bot. VI, 14:388. 1882.
[9] Fournier, in Mart. loc. cit. 204. 1885.

that nearly all subsequent authorities are in agreement as to its conjunction with that group of species. Both *Funastrum angustissimum* (Anderss.) Fourn. and *Cystostemma umbellatum* Fourn. are here made the bases for monotypic series of subg. CERAMANTHUS.

The most recent treatment of Asclepiadaceae as a whole is that of K. Schumann[10] in 'Die Natürlichen Pflanzenfamilien'. The rather generally unsatisfactory aspects of his system are well-exemplified by his handling of the *Sarcostemma* problem. The American species with campanulate flowers were transferred to the Old World genus *Oxystelma* R. Br., leaving in *Philibertia* only those forms with rotate corollas, while *Sarcostemma* was limited to the Old World forms with scale-like leaves. *Oxystelma* and *Philibertia* were placed in the same subtribe (GLOSSONEMATINAE), while *Sarcostemma* and the synonymous genus *Funastrum* were put into different subtribes (CYNANCHINAE and ASCLEPIADINAE, respectively).

Realizing that the species then included in *Philibertia* did not accord with the original description of the genus, Miss Vail[11] proposed for them the new name *Philibertella*. She concurred with Schumann in the disposition of the campanulate-flowered species. However well-meant her intentions, the name only added to the confusion, for it took its place with *Sarcostemma*, *Philibertia*, and *Oxystelma*, all being used for the same species.

The Swedish asclepiadologist Malme[12] also attempted to rectify the error of Schumann by elevating the subgenus CERAMANTHUS Kunze[13] to the rank of genus. But he cited as synonyms, *Funastrum*, *Cystostemma*, and *Philibertella*. It is difficult to understand why Malme chose *Ceramanthus* when several names of generic rank were available; moreover, the name is antedated by *Ceramanthus* Hassk.[14] and *Keramanthus* Hook. f.[15] Fortunately it never was used as widely as were the other current names.

Schlechter[16], in a critical discussion published in 1915, came to the conclusion that the group of rotate-flowered species of the New World was sufficiently distinct to be designated as a genus and he made the requisite combinations in *Funastrum*. At the same time he reinstated *Philibertia* for the campanulate-flowered species.

Most recently, Woodson[17] has returned to the system of Decaisne, uniting *Funastrum* and *Philibertia* with the Old World forms under the name *Sarcostemma*. Redintegration appears to be the only satisfactory way of solving the problem, for the three groups of species are very close, and characters formerly used to separate them are found to break down when all of the species are studied together. It is the course followed in this paper, where the three groups of species constitute sub-

[10] Schumann, in Engl. & Prantl, Natür. Pflanzenfam. 4^2:189–306. 1895.
[11] Vail, in Bull. Torr. Bot. Club 24:305–311. 1897.
[12] Malme, in Arkiv Bot. 4^{14}:2. 1905.
[13] Kunze, in Linnaea 20:26. 1847.
[14] Hasskarl, in Cat. Hort. Bogor. Alt. 240. 1844.
[15] Hooker f. in Curt. Bot. Mag. *t. 6271*. 1876.
[16] Schlechter, in Fedde's Repert. 13:279–287. 1915.
[17] Woodson, in Ann. Mo. Bot. Gard. 28:193–244. 1941.

genera: EUSARCOSTEMMA, CERAMANTHUS, and OXYSTELMA. When once this step is taken, however, a serious question of generic limits arises. If *Sarcostemma* is to be defined as a stable entity, a number of closely related genera must be placed in synonymy.

As even Schumann realized, the Old World *Oxystelma* R. Br.[18] is very close to *Philibertia* HBK., agreeing in such points as the campanulate corolla and the ring of the corona adnate to the corolla-tube. *Oxystelma* is here reduced to the rank of a subgenus of *Sarcostemma*, and it includes the species formerly assigned to *Philibertia*.

The genus *Pergularia* L.,[19] of Africa and Asia, superficially appears similar to *Sarcostemma* in that the corona consists of five inflated lobes and a porrect ring which is free from the corolla. There are numerous points of difference, however, which I summarize in the following table:

Sarcostemma	*Pergularia*
Corolla rotate-subcampanulate, salverform with an inconspicuous tube, or campanulate	Corolla salverform with a conspicuous tube.
Ring of the corona thick and short, entire.	Ring of the corona thin and relatively long, 5-lobed, and denticulate.
Vesicles of the corona obtuse to acute, very rarely attenuate, never spurred.	Vesicles of the corona long and attenuate, spurred.
Pollinium-sac essentially uniformly fertile, the corpusculum radially compressed.	Pollinium-sac with a narrow, hyaline, outer margin, the corpusculum strongly compressed tangentially.
Follicles glabrous to pubescent.	Follicles rather copiously puberulent, usually echinate.

In view of these differences, especially of the pollinium, it would seem best to maintain *Pergularia* as a separate genus. Decidedly it does not seem advisable to complicate further the synonymy of the sarcostemmas by changing them all to *Pergularia*.

There are a number of other genera which have been put into the synonymy of *Philibertia* HBK. and *Funastrum* Fourn., and these must now be regarded as synonymous with *Sarcostemma*. Such are *Pentagonium* Schauer[20] and *Zosima* Philippi[21], monotypic genera, both of which apply to species of the subgenus OXYSTELMA; the latter is a later homonym of *Zosima* Hoffm.[22]. Similarly, *Lugonia* Wedd.[23] was described on the basis of an Andean plant which represents nothing more than an alpine modification, and which is referred also to subg. OXYSTELMA.

Rather perplexing are *Pentacyphus* Schltr.[24] and the very similar *Tetraphysa*

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[18] R. Brown, in Mem. Wern. Soc. 1:40. 1809.

[19] Linn. Mantissa, p. 8. 1767 (not of other authors), cf. N. E. Brown in Kew Bull. 1907:323, who shows that *Doemia* R. Br. is the same as the Linnean *Pergularia*.

[20] Schauer, in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.

[21] Philippi, Sert. Mend. Alt. 29. 1871.

[22] Hoffman, Gen. Umbell. 145, *t. 4*. 1814.

[23] Weddell, Chloris Andina 2:49. 1857.

[24] Schlechter, in Engl. Bot. Jahrb. 37:605. 1906.

Schltr.[25] While they diverge considerably from *Sarcostemma* as exemplified by the type species, the former is sufficiently close to species of subg. Oxystelma to be considered a separate section of subg. Oxystelma, and *Tetraphysa* inevitably follows it.

The following synopsis, then, summarizes the structure of the genus as I view it; and in it I take the opportunity to describe a new section and to make several nomenclatural adjustments for Old World forms which will not be discussed further taxonomically.

- Subg. Ceramanthus
  - Ser. Pannosa — *S. pannosum*
  - Ser. Clausa — *S. glaucum*, *S. clausum*
  - Ser. Cynanchoides — *S. bilobum*, *S. odoratum*, *S. gracile*, *S. crispum*, *S. elegans*, *S. Torreyi*, *S. cynanchoides*, *S. birtellum*, *S. arenarium*
  - Ser. Angustissima — *S. angustissimum*
  - Ser. Flava — *S. flavum*
- Subg. Oxystelma
  - Sect. Philibertia — *S. campanulatum*, *S. Gilliesii*, *S. albiflorum*, *S. solanoides*, *S. stipitatum*, *S. lysimachioides*
  - Sect. Pentacyphus — *S. andinum*, *S. Lehmannii*
  - Sect. Euoxystelma[26] — *S. esculentum*[27]
- Subg. Eusarcostemma[28] — (several species)

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[25] Schlechter, loc. cit. 616. 1906.

[26] **Euoxystelma** R. Holm, sect. nov.: coronae squamae ovoidae apice caudatae incurvatae gynostegium superantes, coronae annulus et columna pubescentes; caudiculae obsoletae. T.: *Sarcostemma esculentum* (L.f.) R. Holm.

[27] Sarcostemma **esculentum** (L.f.) R. Holm, comb. nov. *Periploca esculenta* L.f. Suppl. 168. 1781.

[28] Subg. **Eusarcostemma** (Decne.) R. Holm, stat. nov. Sect. *Eusarcostemma* Decne. in DC. Prodr. 8:538. 1844.

Morphology

All the species of *Sarcostemma* are suffrutescent, dextrorsely twining or trailing vines. In the tropics they may climb high into trees and shrubs, but in alpine or desert areas they are reduced to semi-erect or prostrate subshrubs, variously woody or succulent.

The primary root generally is slightly thickened, forming a slender tap-root. Aerial adventitious roots have been noted in several plants which had been growing in very moist habitats; apparently they are never produced on climbing stems, and but rarely on trailing shoots.

The stems of all the species are more or less woody below and herbaceous above. In temperate latitudes, the plant dies back to this woody base during the winter or dry season. If environmental conditions are harsh, the herbaceous stems may be greatly reduced and either semi-erect or prostrate; or, as in subg. Eusarcostemma, succulent, with the leaves reduced to scales. The plants usually are twining vines, extending from one to more than thirty meters into trees and shrubs.

The woody basal portion of the stem is covered with the ridged, yellow bark of loose texture which is more or less characteristic of the Asclepiadaceae. This bark is first produced at the nodes where there may be corky knobs or ridges decurrent upon the internodes. Above these first few centimeters, the stem is gray- or yellow-green and may be pubescent or glabrous. Even in the latter case, there is usually much pubescence in the axil of the leaves and on the buds. In some species, the young stems are extremely pubescent, becoming less so at maturity.

The number of lateral branches normally produced is variable, but is a good character for several groups of species. When the plant branches profusely, the lateral branches usually are intertwined with each other and the main stem. There seems to be little correlation between the amount of branching and the type of habitat, although plants growing in the open tend to be more branched.

The leaves in *Sarcostemma* are entire and opposite and, on the monopodial portion of the stem, they are strictly decussate. After an inflorescence has been produced, the stem becomes sympodial *(vide infra)* and the leaves of each sympodium member no longer are at right angles to those at the floriferous node next below. By far the majority of the species have cordate leaves with characteristic palmate or pedate venation. As a rule, leaf shape can be used to distinguish groups of species, but there is much variation in the length/width ratio. In the desert species of Eusarcostemma, the leaves are reduced to scales which sometimes are difficult to find, for they wither rapidly. In this connection, it is interesting to note that in S. *clausum*, and less frequently in S. *glaucum* (subg. Ceramanthus), of the dry, coastal habitats of western Peru and Colombia, the leaves often are much reduced in size. In these species, as well as in S. *cynanchoides* ssp. *Hartwegii* (of the same subgenus, but occurring in arid, southwestern United States), the leaves sometimes are caducous, the aspect of the plant then being superficially much like that of a slender S. *viminale* (Eusarcostemma).

Most commonly, the margins of the leaves are entire and somewhat revolute, but they are undulate in several species of two subgenera. This condition apparently is caused by the continued proliferation of the lateral meristems of the leaf after interstitial growth has ceased, and is quite variable in intensity. In S. *crispum*, strikingly undulate leaves are the rule in Texas, but the degree of crisping is much less to the south and west where there actually may be no sign of it. Greenhouse plants of S. *pannosum*, which has less pronounced crisping, may have distinctly undulate and quite plane leaves upon the same shoot.

In nearly every specimen, one finds at the base of the leaf on the ventral surface of the point of juncture of the main veins, a number of small, digitiform structures referred to as "glands" in the taxonomic literature (fig. 1). They are yellow or orange in color and vary in size with the vigor of the plant. In desert

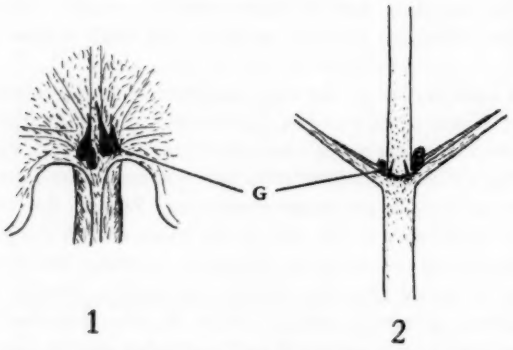

Fig. 1. Foliar glands: 1, base of blade; 2, node; G, gland.

species they usually are reduced in size or occasionally absent. Similar "glandular" structures are found at the nodes, lateral to the petioles, where their position and arrangement suggest that they are reduced stipules; this view is further supported by the fact that occasionally they are slightly laminate. The foliar "glands" are of no taxonomic significance, and their morphological or physiological importance is uncertain. As in the Apocynaceae, the petioles are connected by an interpetiolar ring which appears as a fleshy excrescence of the subjacent internode (fig. 1). The petiolar "glands" are inserted upon the edge of this ring, which also may be puberulent, especially adjacent to the petioles. When the stipular appendages are lacking, there often are tufts of hairs in a corresponding position.

There now can be little doubt that the inflorescence in the Asclepiadaceae is basically terminal, despite the considerable controversy which has taken place in the past. Anatomical, morphological, and experimental studies[29] are fairly clear

[29] cf. Demeter, in Flora 115:130–176. 1922; and Schoute, in Rec. trav. bot. Neerl. 34:182–204. 1937, each with a comprehensive bibliography.

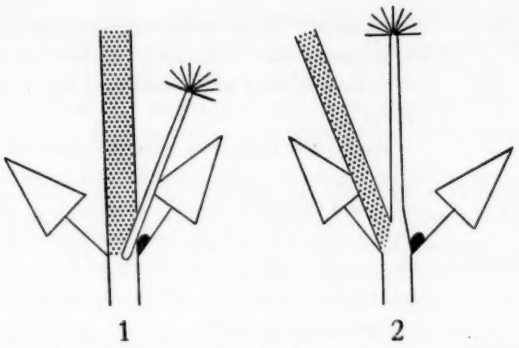

Fig. 2. Diagrams of inflorescence-bearing nodes: 1, actual appearance; 2, morphological interpretation; shading indicates axillary growth.

on this point. The axis which continues the growth of the plant after the first inflorescence arises from one of the buds of the last vegetative node, as is diagrammed in fig. 2. According to the unfortunately highly formalized interpretation of Schoute[30], subsequent sympodium members arise from the axils of the β-prophylls. This is only another way of stating that, with continued inflorescence production, each succeeding internode arises from one of the first two, opposite, leaves ("prophylls") of the node next below; there are, of course, no more than two leaves on this shoot.

Inspection of a vegetative shoot of *Sarcostemma* (fig. 3) shows that the buds in the axils of the paired leaves differ markedly in size; in fact one may be absent altogether. This is the rule in the Asclepiadaceae. If we consider the small buds and large buds separately, we find that they form two opposed spirals with 90° divergence. The first inflorescence terminates this monopodial axis, but is pushed aside by the vigorous growth of the large bud of the last leaf-pair. This shoot forms the first sympodium member, as the upper portion of fig. 3 indicates. The small bud in the axil of the other leaf sometimes grows, but rarely equals the main shoot. The reproductive phase, once initiated, continues indefinitely, each sympodium member bearing two leaves and an inflorescence. The rectangular crossing of the leaves is replaced then by a skew-crossing, for two of the angles between rows of leaves are obtuse and two are acute. As a result, the inflorescences, which are interpetiolar but nearest the large bud of the associated pair of leaves, are borne in two nearly straight rows on opposite sides of the stem, diverging from one another at 150–180°. The bud near the inflorescence is, of course, that which formerly was denoted as a "small" bud, for the large bud has become a sympodium member. A disturbing feature is the presence of an additional bud in the axil of the leaf which presumably subtends the main axis. This bud, which Schoute[31] dismisses as a "small accessory bud," I take to be of the nature of those which are present in such genera as *Juglans*, and which also have been reported for the

[30] Schoute, loc. cit. 1937.
[31] Schoute, loc. cit. p. 187. 1937.

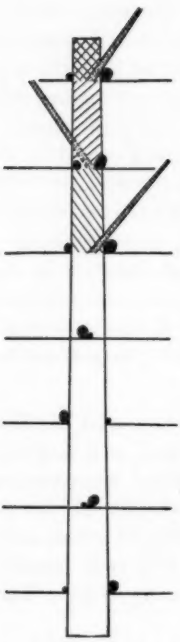

Fig. 3. Diagram of portion of stem of *Sarcostemma* showing large buds and small buds and arrangement of the inflorescences; shading indicates successive internodes of axillary growth.

Apocynaceae. In *Sarcostemma,* the presence or absence of the accessory bud varies both between and within species. Its absence appears to be correlated with a desert or open habitat.

Should the vegetative phase be resumed after a period of inflorescence production, the axis again becomes monopodial and the leaves strictly decussate. It is hardly necessary to add that the torsions introduced by the voluble habit greatly obscure the details of inflorescence and leaf arrangement which are sufficiently difficult to follow on the stem of erect forms.

This condition of the inflorescence is a general one throughout the Asclepiadaceae, and may be noted even in such modified forms as *Stapelia.* In those genera where the inflorescence appears to be axillary, it may be interpreted as terminal according to Schoute. Very rarely, as in *Sarcostemma angustissimum,* the inflorescence actually is terminal to the main axis or a lateral branch. Only one floriferous lateral branch is produced at a node in the latter case. It appears plausible to consider this a case of reduction and specialization, rather than one of primitiveness.

The type of inflorescence is quite variable in *Sarcostemma.* Usually it is umbelliform in subg. CERAMANTHUS and racemiform in EUSARCOSTEMMA and OXYSTELMA. The basically cymose nature of the inflorescence is demonstrated by the irregularly centripetal development of the flowers and by the arrangement of the flowers upon the floriferous axis.

In the subg. CERAMANTHUS, the type of inflorescence has been used to distinguish four series. *Sarcostemma pannosum* is placed in a series by itself since the inflorescence always is manifestly compound. The nodeless peduncle may dichotomize in extreme cases producing two cincinni, each more than a centimeter in length. Upon the axis the flowers are disposed spirally in pairs.

A second series includes S. *clausum* and S. *glaucum* in which the peduncle ordinarily equals or exceeds in thickness the axis below the inflorescence-bearing node. Frequently it bears two catenulate cymes; the inflorescence is umbelliform, all the flowers appearing to come from about the same place, but blooming in an irregularly centripetal fashion. The second cyme, if present, is lateral and sessile upon the peduncle.

Most of the species of subg. CERAMANTHUS fall into a third series in which the inflorescence is umbelliform and is borne upon a slender peduncle which only very rarely equals the stem in thickness or bears a secondary cyme. *Sarcostemma angustissimum* is placed in a monotypic series on the basis of its terminal inflorescence; the peduncle is short or absent, but when present is not equal to the stem in thickness.

The inflorescence in subg. OXYSTELMA most commonly is racemiform, although the superficial appearance of occasional individual plants may belie their structure. Thus while all of the species with racemiform structure may experience such abbreviation of the floriferous axis as to simulate the umbelliform type in one or more inflorescences, comparison of a number of inflorescences, or careful examination of the peduncle for bracts, will reveal the racemiform nature. On the other hand, *Sarcostemma solanoides* presumably never deviates from the strictly umbelliform inflorescence. *Sarcostemma* (§ PENTACYPHUS) *andinum* apparently illustrates reduction from the racemiform type along different lines: invariably there are two nodes in the inflorescence, each of which bears a single flower. Again it must be realized, however, that specimens of species with typically racemiform inflorescences (which have the flowers arranged in pairs along an axis of several nodes) may assume this appearance. The nature of the inflorescence has not been used to delimit series in OXYSTELMA since the species do not seem to fall into natural groups along these lines.

In all the species of *Sarcostemma*, there is a tendency for a more or less specialized reproductive portion of the axis to be developed. This condition is most clearly seen in *S. clausum* and *S. glaucum* where the inflorescences may be borne upon long, lateral branches which have reduced leaves, the whole resembling the compound inflorescences of certain species of *Cynanchum (Tassadia)*.

Length of the peduncle is a character which has been used with disastrous results in the past, as a glance at the synonymy of *S. clausum* will testify. Many of the segregates of that species were based upon slight differences in the length of the peduncle relative to the associated leaves. Within several species the peduncle may be much longer than the leaves or absent entirely. In certain species, however, the extreme conditions are valid characters, e. g. in *S. elegans* vs. *S. Torreyi*.

Few distinctive features are presented by the pedicels. Relative number, thickness, and length are of some value in setting apart groups of species, but have little practical use. The pedicels elongate gradually until anthesis, and if fertilization takes place and a fruit is formed, the pedicel and peduncle enlarge to support the follicle.

The calyx in *Sarcostemma* is gamosepalous, and the lobes are divided nearly to the base. The upper surface usually is glabrous, but the lower varies from glabrous to densely pubescent. In many cases, especially in subg. CERAMANTHUS, the marginal hairs are long, making the lobe ciliolate. Within the calyx tube, generally distributed about the base or alternating with the lobes, are one or more digitiform

structures commonly called "glands." These apparently are homologous with the calycine squamellae of the Apocynaceae which have been interpreted as being of stipular origin[32]. In the apocynaceous genera studied, they were correlated with the nature and arrangement of the stipules and were constant within a genus or subgenus. No such correlations have been noted in *Sarcostemma;* the number and distribution of the squamellae are variable and without taxonomic significance. A squamella consists of a central core containing many druses and an outer, deeply-staining, palisade epidermis.

It would appear that where reduction in size of certain structures has proceeded to a given point, they assume this more or less cylindrical, translucent, lutescent appearance of the "glands." This may be noted, for example, for the stipules. Occasional aberrancies also are suggestive: in one specimen of *S. clausum*, a single calyx lobe had a "glandular," lateral appendage at the base: in *S. angustissimum*, the minute calyx lobes are "glandular" at the apex; in *S. lysimachioides*, the squamellae are borne in groups at the margin of a triangular pad of tissue alternating with the calyx lobes; finally, in those species with mucronate leaves, the mucro often is strikingly similar to the various "glands" in appearance. On the other hand, there is some indication that the multicellular hairs found upon the interpetiolar ring and the calyx lobes may become "glandular" in appearance. The whole problem is one which would repay investigation, for upon its solution depends our interpretation of the calycine squamellae and the appendages of the leaves.

The corolla is gamopetalous, and the degree of cohesion of the lobes is an important taxonomic character. In general, species of subg. OXYSTELMA have very broadly campanulate corollas which are shallowly lobed; in the angles of the sinuses there often are minute petalaceous teeth. The corolla in subg. CERAMANTHUS and EUSARCOSTEMMA is rotate-subcampanulate or salverform and is divided nearly to the gynostegium. The corolla lobes usually are spreading or ascending, but they may be strongly reflexed.

It is the behavior of the androecium and gynoecium which characterizes the Asclepiadaceae as a family, hence it will not be amiss to describe in some detail the morphology and anatomy of the structures in these two floral whorls. The material on which the following discussion is based consists of longitudinal and cross sections of flowers and buds; extensive use also has been made of flowers and buds cleared in 5 per cent sodium hydroxide solution and treated with lactic acid. The latter technique is especially useful, for the sodium hydroxide removes all coloring material from the tissues rendering them transparent; the cell walls, however, are undistorted and may be studied with or without the application of a stain.[33] In such preparations, the course of the vascular bundles may be followed *in situ* and a clearer concept of the spatial relations of the various parts may be obtained without the laborious method of reconstructing from a series of sections.

[32] Woodson, R. E., and Moore, J. A., in Bull. Torr. Bot. Club 65:135–166. 1938.

[33] This technique is described in A. S. Foster's 'Practical Plant Anatomy,' 1949. Staining is discussed by Thomas Morley in Stain Techn. 24:231–235. 1949.

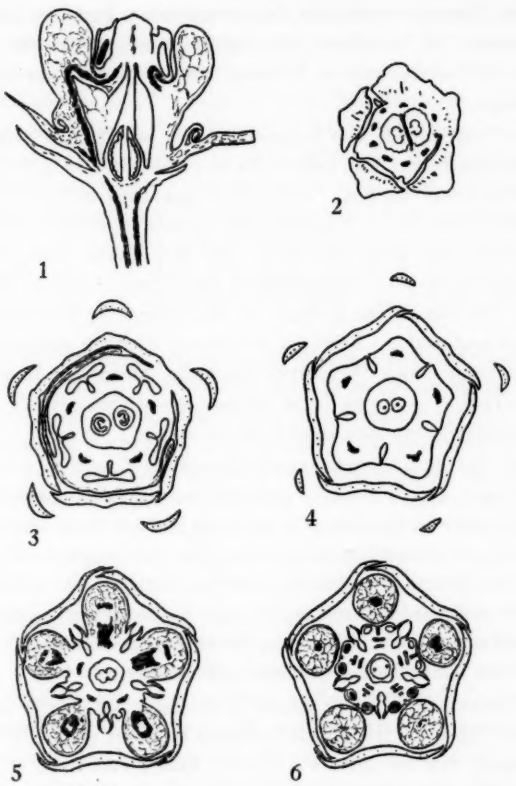

Fig. 4. Longitudinal section of flower and cross section of bud: 1, longitudinal section of flower showing vascular bundle of stamen, ring of the corona, and slightly immersed carpels; 2, cross section through receptacle showing sepals, squamellae, and carpels immersed in the receptacle; 3, cross section through the region of the corona ring showing ring, corolla, and the staminal column; 4, cross section through the staminal column showing grooves and the styles; 5, cross section through the region of the corona vesicles showing vascular bundle in the corona vesicles and the anther-wings; 6, cross section through the gynostegium above the attachment of the corona vesicles showing the thecae and pollinium-sacs, anther-wings, and the base of the stigma-head.

Supplementing the description which follows are the semi-diagrammatic drawings of fig. 4 which represent cross sections of a bud, and a longitudinal section of a flower of *Sarcostemma pannosum*. The five antesepalous stamens are borne upon the corolla tube near the base and are coherent laterally almost to their apices, forming an epipetalous tube. The united filaments constitute what commonly is called the column. Externally, the filaments are marked by deep grooves in the

column in subg. CERAMANTHUS and EUSARCOSTEMMA, but these usually are lacking in OXYSTELMA. In S. *andinum*, the margins of the groove are extended at an angle of about 45° to the column, forming two prominent flaps continuous with the anther-wings.

The anthers contain but two pollen-sacs, each of which is visible dorsally as an elongate protuberance. The connective is prolonged into a short spike which supports a membranous margin. This apical appendage of the anther usually is appressed to the stigma-head. Ventrally, the anthers are coherent by their margins except for a short distance at the apex. The five sinuses thus produced in the staminal tube expose the receptive surface of the stigma, as will be discussed below. Laterally also, but abaxial, the margins of the anthers are produced to form the anther-wings or anther-alae. These are continuous with the margins of the groove in the column from which they differ markedly, however. Histologically, the transition is marked by a change in the composition of the cell walls as is indicated by their greater affinity for basic dyes (e. g. safranin).

Morphologically, the anther-wings are characterized by their cartilaginous texture and appearance, and by the fact that they are produced somewhat beyond the margins of the groove in the column. They are inclined at an angle of about 45° to the plane of the thecae and are recurved so that their edges are closely appressed. Towards the base there is an opening into the so-called alar chamber delimited ventrally by the conjoined anthers and laterally by the anther-wings. This orifice varies in size and shape from thin and narrow to large and circular. It is the opening into which the instrument of pollination is introduced.

As in all Cynanchoideae, the stamens at maturity are closely connivent with the united stylar region of the carpels (referred to as the stigma-head). While it is stated commonly that the anthers are merely loosely connivent with the stigma-head or united only by their tips, neither of these descriptions is accurate. The young anthers are at first free from the gynoecium. Fairly early in their development, however, the ventral surface of the staminal tube bulges to form a pronounced flange about the circumference of the staminal tube at the level of the locules. This flange in later development becomes closely appressed to the lower surface of the stigma-head and the tissue of the two structures finally becomes joined. It can be seen in sections of the flower that the cells of one dovetail between those of the other and that there is a slight crushing and disruption of the superficial layers. In this area, the highly differentiated, columnar epidermis of the stigma-head is unchanged in the bud stage, but by the time of anthesis, the cells have lost their characteristic rectanguloid shape and their strong affinity for stains. The anthers are free from the stigma-head around its entire circumference except at the flange. The lateral surface of the stigma is exposed, however, only at the five sinuses in the staminal tube, which are hidden within the alar chambers.

We come now to those structures of the androecium which collectively make up the corona. Woodson[34] has pointed out the dangers of lack of precision in the use of the word corona, which he rightly applies to "various elaborations or enations of the staminal filaments only." That definition is followed in this paper for the reason that there are at least three structures which have been, or could be, interpreted as corona in *Sarcostemma*. It is customary to speak of inner and outer corona, but there is no assurance that the "inner corona" of one group is not the equivalent of the "outer corona" of another, nor that it will not be mistaken for such by the user of the, at first sight, obvious key character. In many genera of the Asclepiadaceae, there are three appendages of the stamens, as well as others of the corolla, so that any distinction of "inner" or "outer" corona becomes impossible.

In nearly all the species of *Sarcostemma*, there is a so-called "outer corona" or "faucal annulus." Whether this structure pertains to the corolla or to the androecium is not easy to determine; indeed, I am not certain what evidence could be considered definitive in the light of recent studies of the development and initiation of floral parts. The ring of the corona is best studied in the species of the subgenera CERAMANTHUS and EUSARCOSTEMMA, where it reaches maximum development. In subg. OXYSTELMA, the ring is present but usually abbreviated or adnate to the corolla. The corona ring may be a ridge at the base of the staminal column or a thick, revolute fold of tissue free from the corolla except at the very base. In many species, the ring is adnate to the androecium directly below the anthers; in others it is adnate to the corolla; finally, there are species in which the ring is adnate both to androecium and corolla. Cross and longitudinal sections show that the ring is more or less double at maturity and is composed of the same type of rather loose parenchyma as are the corolla and corona vesicles borne upon the filaments. No vascular supply is present, nor does the staminal trace diverge from its course in the direction of the ring. Viewed superficially, the corona ring is similar in texture to the androecium and not to the corolla. In subg. OXYSTELMA, § EUOXYSTELMA, both the column and corona ring are often puberulent, while the corolla is glabrous.

In the hope that developmental studies might shed some light on the problem, sections of buds and buds of varying age, cleared with sodium hydroxide, were examined. The later development of the flower studied here is remarkably similar to that described by Boke[35] for *Lochnera rosea*. As in that species, it is possible to distinguish two portions of the corolla tube: that below the insertion of the stamens, and that above this point. The lower corolla tube in *Sarcostemma* appears to be of receptacular origin, as is the case in *Lochnera*. The corolline traces do not branch until they reach the point of staminal insertion, whereupon two laterals depart simultaneously from each, run periclinally to the margins of the lobe, finally

[34] Woodson, in Ann. Mo. Bot. Gard. 28:199. 1941.

[35] Boke, Norman H. A series of three papers in Am. Jour. Bot. 34:433–439; 35:413–423; 36:535–547. 1947–1949.

to pursue their customary course upwards. A number of secondary branches from the distal margin of the horizontal portion of the laterals supply most of the mesophyll of the corolla lobe. Distal to the androecium, the upper corolla tube appears to be the result of ontogenetic fusion of separate lobes. The two lateral veins are closely appressed and traces of former epidermal layers often can be made out, especially near the sinus. The proximal portion of the upper corolla tube is slightly thickened by an adaxial meristem of the sort noted by Boke.

Unfortunately, the origin of the corona ring is not clarified by a study of development because of its early association with both the upper corolla tube and the staminal column. As nearly as I can determine, it arises in the angle of the sinus formed by the insertion of the stamens upon the corolla. Opposite a stamen, the ring appears first as a protuberance from the column; opposite a corolla lobe it appears in the sinus (in the bud stage).

Though the evidence is by no means clear-cut from this preliminary work, I am of the opinion that the corona ring must be considered a part of the androecium if we are to attempt to assign such structures to one of the formal categories of descriptive morphology. Comparison of *Sarcostemma* with a number of other forms in the Cynanchoideae shows that many have a tendency, expressed to a greater or lesser extent, for the base of the staminal tube to flare out into a corona ring, e. g. *Fischeria*, *Gonolobus*, and other genera, especially of the Gonolobeae. Perhaps the corolline faucal annuli of such forms as *Stapelia* and *Periploca* are the result of growth of the adaxial or ventral meristem discussed by Boke and Troll.

The so-called "inner corona" is composed of five vesicular outgrowths of the filaments directly below the anthers. Since the corona, as I interpret it, comprises both the ring at the base of the column and these enations of the filaments contiguous to the anthers, I shall refer to its components as corona ring and corona vesicles. The vesicles are constituted of a loose parenchyma which becomes distorted during later growth. They arise late in ontogeny so that in a bud, even shortly before anthesis, they may be quite small. Incidently, this has led to the description, in other genera, of species "*parvicoronata*," etc. based on nearly mature buds. Towards the base of the vesicle, the staminal trace usually arcs strongly upwards into the corona segment before reaching the anther.

The corona vesicles arise as small protuberances increasing in size gradually by interstitial growth, for the most part. Shortly before anthesis, rapid growth ensues, principally in the epidermal and immediately subjacent layers. The deeper-lying cells are stretched to form an aerenchyma and may be grotesquely twisted. Probably it is the inclusion of innumerable intercellular spaces filled with air which gives to the vesicles their characteristic, almost crystalline, appearance.

The corona vesicles are quite variable in shape. At the opening of the flower they are ovoid or obovoid, occasionally somewhat quadranguloid or laterally compressed. The upper end is rounded, truncate, or pointed; frequently there is an apiculation on the inner side at the apex. In subg. Oxystelma § Euoxystelma,

the corona vesicles are attenuate apically, forming long, incurved processes exceeding the stigma-head. Towards the base, there may be manifest a decided constriction above the attachment of the vesicle to the column. The latter forms a sort of platform supporting the vesicle in many species.

Variation in the corona vesicles has been much over-emphasized taxonomically in the past, although the dangers of such a course have been stressed by most authorities on the family. Examination of herbarium material of all the species, supplemented by greenhouse and field observation of a number, has convinced me that, while the corona-shape potentialities are constant in the species recognized here, developmental upsets of one kind or another may modify their actual shape considerably, especially in subg. OXYSTELMA (cf. S. *Gilliesii* and S. *campanulatum*). The presence or absence of an apiculation, or the degree of compression, must not be overly stressed where individuals are concerned.

All these elaborations of the androecium apparently have arisen as a result of natural selection operating in conjunction with entomophily. The method of pollination recently has been described and illustrated for *Asclepias*[36] and a detailed discussion is not necessary here. The essentials of the process are well known, but a clear understanding must await sedulous biological study. It is speciously simple to assign roles to the various components of the complicated flower, but many aspects will have to be re-examined. For example, it is seldom realized that in most cases the corona and other floral appendages serve not so much to attract insects as to guide their legs into the proper position for pollination. In its search for the abundantly secreted nectar (which is well advertised by a heavy fragrance), an insect scarcely can avoid getting its feet or various bristles upon its body caught in the anther-wings at the basal opening. Once caught, there is no escape without withdrawing a pollinium.

According to the terminology which I shall employ, each pollinium consists of two pollinium-sacs which are joined by the translator arms (or caudicles) to the corpusculum. The translator arms and the corpusculum, sometimes called the "gland," make up the translator apparatus. Each pollinium-sac consists of the contents of one locule of the anther, enclosed by a yellowish, elastic substance of a waxy appearance. This investing layer about the pollen apparently is secreted by the tapetum at an early stage in development. The pollinium-sac is essentially oblongoid-cylindrical, but gibbous in outline, and the more strongly curved edge is toward the connective of the anther. At the time that the pollinium-sacs are being formed, the glandular surface of the stigma-head is secreting a substance not unlike that surrounding the pollen. While this process has been described both in English[37] and in German[38], the details are not known widely. The essentials have been confirmed for *Sarcostemma*. The result of this secretion, deposited at

[36] Woodson, op. cit. 198–199. 1941.

[37] Corry, Thomas H. Structure and development of the gynostegium and the mode of fertilization in *Asclepias cornuti* Decne. (*A. syriaca* L.), Trans. Linn. Soc. II, 2:173–207. 1884.

[38] Demeter, Karl. Vergleichende Asclepiadeenstudien. Flora, n. s. 15:130–176. 1922.

varying rates and times, is the translator apparatus, one of the most remarkable structures in the plant kingdom.

That portion of the stigma-head above the alar chamber is creased by a furrow along the same axis as the anther-wings. The margins of this furrow secrete first and they form two bars of a substance which, initially soft and yellow, hardens and becomes deep brown. Subsequently the entire furrow begins to secrete, and the two bars thus become connected at the back by a thin plate. At the same time, however, the stigma-head is developing and slowly changing in size and shape: by differential growth, the margins of the furrow and their secreted bars are pushed forward and toward one another as the furrow increases in size at the back. The corpusculum at this stage is in the form of a clip, the free ends curving inwards. It is easy to see, then, why the name "gland" is inappropriate for the corpusculum, for it not only secretes nothing itself but is scarcely adhesive as was formerly believed.

Rather late in development, two bands of tissue of the stigma-head, extending from the corpusculum to the pollen-sacs of contiguous anthers, secrete the material which forms the translator arms. Because of their relative thinness, the translator arms clearly show the imprint of the epidermal cells which secreted them; the result is that they appear cellular to superficial observation. The corpusculum, on the other hand, is so thick that it is only in sections or whole mounts cleared in lactic acid that one can discern the slender bars of secrete of which it is constituted. In carefully made sections these may even be referred to the cells from which they were produced.

Several days before the bud opens, the ventral wall of the anther begins to disintegrate across a relatively wide area at the apex of each locule and this continues until each pollinium-sac is exposed at the back. The distal end of the caudicle, being the last portion to be secreted and protected from desiccation, is still soft and adhesive, and it apparently contacts the upper corner of the pollinium-sac and fuses with it. In *Sarcostemma,* there is a perceptible joint between the two separately formed structures. In other genera, however, the translator arm merges gradually with the substance of the pollinium-sac envelope. At the time of anthesis the translator arms are soft and flexible, and because of a difference in thickness of the secreted material and of the curvature of the stigma-head have developed a torsion which causes them to turn at right angles to the plane of the corpusculum, when removed from the flower. By this motion the attached pollinium-sacs are caused to rotate 90° so that the more convex side is turned toward the back. Thus it comes about that the two bags of pollen lie in parallel planes instead of in the same plane as they did in the flower.

The corpusculum usually is broadly sagittate, but may be narrowly so, or ellipsoid. As a consequence of the method of its secretion, it is canaliculate and the canal, in the form of a cone, is open along the front forming a cleft. The latter is aligned with the alar chamber so that if a bristle of the proper size is introduced into the alar chamber at the base and pulled upward, it is drawn into

the corpusculum and wedged firmly in the cleft. When withdrawn from the flower, the bristle then carries with it the pollinium, the two pollinium-sacs rotating slowly as the caudicles dry. Should the same bristle be inserted similarly into another alar chamber, it is the translator arm attached to one pollinium-sac which is caught in the anther-wings, while the other remains outside of the chamber. At the top of the alar chamber the pollinium-sac is abruptly caught against the projecting stigma-head and it breaks from the translator arm. The latter, thus freed, passes into the cleft of the corpusculum of the new pollinium, which is then withdrawn. This process of insertion and removal produces the dichotomous or unilateral combinations of pollinia called multiple pollinia. I have observed multiple pollinia composed of more than twenty pollinia; and, in one instance, a small insect formed a bridge between two pollinia.

Judging from the relatively high frequency with which they occur in the species which I have examined, multiple pollinia are a regular and natural occurrence in many asclepiads. Robertson[39] has discussed the importance of multiple pollinia to species of *Asclepias* with large gynostegia which catch fewer processes on an insect's leg. In such cases, they afford a greater chance of insertion since broken caudicles appear to be more easily caught than insect bristles and since the long multiple structures are guided more efficiently into the anther-wings by the corona segments. By means of multiple pollinia an insect can carry many more pollinia than the available bristle space would allow were each bristle to bear but one corpusculum.

When described, the process of pollination seems hopelessly complex and laborious, yet when the proper instrument of pollination is employed it is surprisingly easy to perform. In *Sarcostemma bilobum* ssp. *Lindenianum*, for example, where the orifice of the alar chamber is sufficiently large to admit a fine dissecting needle, I have produced multiple pollinia with little difficulty; a fine hair is suitable for species with smaller flowers. Brown[40] and Robertson[41] have noted the amazing rapidity with which the proper insect is able to effect pollination. Often the action is quicker than the eye can follow. If one watches the flowers for even a short period he is certain to see many insects, attracted by the sweet fragrance, crawling over the umbels of flowers and probing for nectar among the corona segments. The weight of the insect makes the flower, or entire inflorescence, suddenly top-heavy, and, as it begins to tilt, the insect grasps the only structures which afford support, the projecting anther-wings. Rarely is an entire leg caught by the alar chamber; usually only a bristle or row of setae upon the leg or abdomen slips into the orifice, and with a single swift movement of the insect, a pollinium is withdrawn. Pollination is only slightly more difficult, requiring the insect to give an extra tug which breaks the pollinium-sac from the caudicle.

[39] Robertson, Charles. Insect relations of certain Asclepiads. I. Bot. Gaz. 12:214. 1887.
[40] N. E. Brown, in an appendix to Corry, op. cit. 1884.
[41] Robertson, Charles. Notes on the mode of pollination of *Asclepias*. Bot. Gaz. 11:269. 1886.

I should mention that in *Sarcostemma* the majority of mature flowers taken from herbarium specimens were found to have been pollinated at least once. Usually no more than three pollinia are inserted into the alar chambers of a single flower, but it is by no means uncommon to find a flower completely pollinated. Only very rarely have I seen a single pollinium-sac removed from its locule with the other still in place, and I have never observed a pollinium-sac which had produced pollen tubes while still within the locule.

It would appear that cross-fertilization is the rule in those species of Asclepiadaceae which have been studied. Some, like *Asclepias syriaca*,[42] *A. curassavica*, and *A. nivea*[43] are self-sterile. In others it appears likely that the behavior of the translator arms in turning the pollinium-sacs into the right plane for insertion between the anther-wings, a matter of one or two minutes time, would lead to cross-pollination, even if there were no other mechanism for insuring this.

The family Asclepiadaceae has been divided into two sharply distinct subfamilies on the basis of the structure of the translator apparatus and related floral differences. The pollinia of the Cynanchoideae, described in preceding paragraphs, may be visualized to have evolved from simpler structures in the Periplocoideae and Apocynaceae according to the interesting studies of Demeter.[44] In the genus *Apocynum* (Apocynaceae), the first semblance of a translator apparatus is found. Here the stigma-head secretes five thin, quadrangular plates which alternate with the stamens. These are enclosed within cartilaginous margins of the anthers (similar to the anther-wings) and are adhesive, catching the pollen which is discharged from the anthers in tetrads. This pollen-bearing structure then becomes stuck to the appendages of insects which visit the flowers and thus disperse the pollen.

The Periplocoideae also discharge the pollen in tetrads. The latter fall from the anthers into rather complicated translators which are divided into three parts: an upper spoon- or cone-shaped structure which is adhesive and contains the tetrads, a lower adhesive disc which becomes attached to the insect, and a central connecting stalk. After studying the method of formation of the translator and certain teratological forms, Demeter[45] concludes that the spoon or cone is homologous to the corpusculum and that the adhesive disc is comparable to laterally conjoined translator arms. Changes in the shape of the stigma-head and in the distribution of the secretory cells can be imagined which would lead to the formation of a typical pollinium.

Although the occurrence of pollen grains grouped into tetrads is scattered throughout the flowering plants, the formation of pollinia has been reported only for the Asclepiadaceae, the subfamily Mimosoideae of the Leguminosae, and the

[42] *cf.* Stevens, O. A. Cultivation of milkweed. N. Dak. Exp. Sta. Bull. 333. 19 pp. 1945; and Sparrow, K. K. Types of pods of *Asclepias syriaca* found in Michigan. Jour. Agr. Res. 73:65–80. 1946.

[43] I have been unable to self-pollinate or to hybridize *A. nivea* or *A. curassavica* in the greenhouse, despite repeated attempts.

[44] Demeter, op. cit. 174. 1922.

[45] Demeter, loc. cit.

Orchidaceae. In the Chlaenaceae, a small family of the Malvales, there are multiple groups of four or sixteen pollen grains enclosed within a deeply furrowed wall.[46] This wall has been interpreted as the modified spore-mother cell wall, and, if this interpretation is correct, these aggregates cannot be referred to as pollinia (as their describer recognizes). The pollinia of the other three groups are characterized by having the pollen grains merely adherent, with or without a thick matrix, and not enclosed within a single cell wall.

In the Mimosoideae, the pollen is in tetrads or aggregated into pollinia of relatively few grains, in an ovoid mass which bears at the pointed end an adhesive substance apparently derived from the tapetum. The stigma is a simple, obscurely sulcate, capitate structure, and there are no special devices for receiving the pollinia.

The Orchidaceae show an interesting series from pollen in tetrads to various types of pollinia. In the more primitive forms each locule produces many small pollinia similar to those of the Mimosoideae, but these are held together into packets by viscid threads derived from the tapetum. These compound pollinia may be attached by slender, elastic caudicles to an adhesive disc which is the secretion of the rostellum, a sterile portion of the stigma. In certain species, the sticky substance secreted by the stigma is first applied to the head of a visiting insect, and the pollinia subsequently fall from the anthers into this substance and become affixed. Pollinia of the more advanced type are compact, waxy structures borne upon rather specialized caudicles which are attached to an adhesive, cellular disc. In this case, a layer of tissue of the rostellum has abscissed, carrying with it the sticky secretion. The caudicles undergo various movements which put the pollinium into the proper position for pollination.

In general, the pollinia of the orchids are much less specialized than those of the Asclepiadaceae. The rostellum is, in a sense, comparable to the secretory stigma-head, and the caudicles and adhesive disc have been compared with the translator arms and corpusculum of the asclepiads. These similarities are rather superficial, however. Furthermore, the structure of the stigmatic chamber in the orchids is by no means as directly related to that of the pollinia as it is in the milkweeds, a fact which perhaps accounts for the more frequent occurrence of natural hybrids in the orchids in contrast to the asclepiads. On the other hand, in the transformation of the perianth into the most outlandish structures, and in the development of special insect food tissues or of pseudocopulation, the orchids have far surpassed the Asclepiadaceae.

The Asclepiadaceae are often mentioned as illustrating mechanical isolation of species and extreme adaptation for insect pollination, but few persons have realized the delicacy and precision of the relationship. While pollination can easily be accomplished by the right pollinator, it must be emphasized that there are so many elements involved in the process that, if any one is incompatible with any other,

[46] Smith, C. C. A case of "pollinia." Phytologia. 1:83–88. 1934.

it fails. That most assiduous, but apparently almost forgotten work of Charles Robertson[47] has made this quite clear. Precisely to what part of an insect's body a pollinium will be attached is determined by the structure and height of the corona, the length of the column, the structure of the anther-wings, the structure of the stigma-head, the shape of the corpusculum, etc. Robertson[48], for example, found that bumble-bees may have pollinia of *Asclepias Sullivantii* on their claws, of *A. verticillata* on their tarsal hairs, and of *A. longifolia* on the hairs of the ventral surface. These three species, although in bloom at the same time and employing the same efficient pollinator, are nevertheless practically incapable of hybridization. While visiting a flower of *A. Sullivantii*, the bumble-bee deposits only pollinia of that species, because only they are in a position to be inserted and caught in the alar chamber. If it should happen that pollinia of *A. verticillata*, upon the tarsal hairs, were caught between the gaping anther-wings of *A. Sullivantii*, they are so small that they would be withdrawn without affecting the plant in any way. Conversely, the pollinia of *A. Sullivantii*, the flowers of which are about three times the size of those of *A. verticillata*, cannot be inserted into the alar chamber of the latter under the dissecting microscope, much less by the bumbling bee. Similar relationships are found between *A. longifolia* and the other two species; in size, the flowers approach those of *A. verticillata*, but the anther-wings and pollinia have a completely different structure.

Further evidence for the rigidity of the interrelation of flower and insect is provided by the multiple pollinia. I have never found these combinations to include more than one kind of pollinium (and the morphology of a pollinium often is sufficient to define a species in *Sarcostemma*). There is, thus, what might be called a lock-and-key relation between the pollinia and the alar chamber. It is only the proper key, the pollinium-sac, which can be inserted into a given lock, the alar chamber, so that fertilization will take place. Moreover, the key must be in the proper hands to gain access to the lock.

We may inquire into the effects of the intimate relationships between the milkweeds and their insect-pollinators, and although we cannot yet answer the question, we can perceive that the effects are far-reaching ecologically, genetically, morphologically, and taxonomically. The plant is dependent upon a particular type of pollinator, and both the plant and the insects in its environment must have evolved more or less together. *Sarcostemma pannosum*, from western Mexico, when grown in St. Louis was visited by many insects, but no pollinia were withdrawn and no fruit produced. A plant, on the other hand, may have a profound effect upon the insects, aside from that of supplying them with food. It is well known that insects sometimes are caught by the corpuscula which they are not sufficiently strong to remove, and they perish on the flower. Indigenous forms

[47] Robertson, Charles. Notes on the mode of pollination of *Asclepias*. Bot. Gaz. 11:262–269. 1886. Insect relations of certain asclepiads. I & II. ibid. 12:207–216, 244–250. 1887; Flowers and insects, Asclepiadaceae to Scrophulariaceae. Acad. Sci. St. Louis. Trans. 5:569–577. 1891.

[48] Robertson, op. cit. p. 250. 1887.

must be caught rather rarely when one considers that the number of visitors to a single flower runs into very high figures. However, for the hive-bee, introduced into our fauna, the situation is different. In a period of seventeen days, Robertson[49] found 671 dead bees in the flowers of a patch of *Asclepias Sullivantii*. Furthermore, this species, which fastens its pollinia to the claws of insects, may so fetter a bee with pollinia that it is expelled from the hive as a result of its inability to collect honey and to climb upon the combs. Of course, *A. Sullivantii* is not benefited, for, as Robertson puts it: ". . . it seems that the flowers are better adapted to kill hive-bees than to produce fruit through their aid."

Genetically, a situation results in which the species are isolated mechanically from hybridization with one another, yet usually are cross-pollinated with other individuals of their own species. Two species, then, as isolated as if one had migrated into a different habitat, may respond with striking specializations in floral structure but undergo little or no change in vegetative organs. One need only compare species of *Gonolobus, Marsdenia,* and *Cynanchum* from Mexico or South America to see that often only slight differences, in the structure and arrangement of the trichomes, for example, distinguish them vegetatively. Yet the floral differences are so great that they are used to characterize categories of tribal rank.

This field of inquiry is one which still scarcely has been touched. It will require much patient field work before a picture of the dynamics of any one species can be worked out. A taxonomic monograph can serve to indicate some of the problems, however, and should function as a framework, albeit flexible, within which they are interpreted. It is of considerable interest to note that in several closely related species of *Sarcostemma* which occupy the same or contiguous areas, there are differences in the shape of the pollinium-sac and corpusculum and complementary differences in the anther-wings which would make hybridization very difficult. If one examines the key to the species of the series CYNANCHOIDES, he will notice how many groups of species are segregated by differences in the structure of the pollinium, the length of the column, or the degree of apiculation of the stigma-head. This, in all probability, explains the rarity of hybridization and those evolutionary processes associated with introgression which are proving to be of such importance in other families of plants and animals. Certainly the Asclepiadaceae offer fascinating subjects for the evolutionary biologist.

The conjoined stamens and gynoecium make up a structure called the gynostegium, the name referring to the fact that the androecium completely roofs over the carpels. The stigma-head exposed at the top is more complicated than might appear at first sight. The apex is papillate and may be obscurely bilobed or bear two long apiculae. The degree of apiculation, however, is somewhat variable, and characters of the stigma-head must be used with discretion. The rather massive body of the stigma-head contains two central strands of short, spirally thickened cells. These are a continuation of the vascular strands of the styles which gradually

[49] Robertson, op. cit. p. 211. 1887.

attenuate toward the apex only to enlarge within the stigma-head to form a core of considerable dimensions. Their function appears to be to support and to strengthen, since in other genera they extend nearly to the surface and, flaring broadly, form a subepidermal layer of sclereids.

The papillate apical portion of the stigma-head is distinct from a lower, non-papillate region which projects, shelf-like, laterally. On the upper surface of this area are the five furrows in which the corpuscula are secreted. Lateral to these are the less prominent grooves in which the translator arms are produced. Below this region the stigma-head is abruptly constricted to the styles. Upon this lower surface is the receptive surface of the stigma and below this, the attachment of the flange of the staminal tube.

Corry[50] has stated that the receptive area of the stigma-head is a continuous ring, similar to that in the Apocynaceae, above the attachment of the staminal tube. Whether or not this is so can be determined only by laborious experimentation; the fact remains that the stigma-head is functionally receptive only at the five points which are accessible to the alar chamber, i. e. alternating with the stamens. In order for pollination to be effected, a pollinium-sac must be drawn between the anther-wings at the base and up against the stigma-head where it breaks from the caudicle. In many species there are projecting ridges within the alar chamber which firmly grip the pollinium-sac and hold it in the proper position. In this moist chamber, the pollen tubes grow, in the form of a skein, into the stigma and down the styles to the ovary. Although apparently all of the pollen grains germinate, the pollen tubes are found to escape only from a rather small area along the more convex edge of the pollinium-sac, which is always the edge towards the stigma in the alar chamber. This occurs whether they are germinated in the flower or in a sugar solution.

The two carpels are free nearly to the base and are somewhat sunken in the receptacle. Alternating with them are two small papillae, the nature of which is completely unknown. Devoid of vascular tissue, they may be the result merely of compression of the receptacular tissue by the confining corolla tube, or the vestiges of carpellodes. Very rarely one finds that three carpels have been produced, but conditions within the lower corolla tube are so crowded that it is difficult to determine if the small papillae still are present. The anatropous ovules are borne upon axile placentas and the micropyles are directed outwards.

Ordinarily only one carpel of a pair develops into fruit, although two is the rule in several species. The paucity of fruit, as compared with flowers, has been attributed to difficulty in pollination. This clearly is not the case in the forms which I have studied, for not only is pollination a simple matter for the right insect, but it is not uncommon to find inflorescences in which a majority of flowers have young fruit. Yet, in these same species, only a single follicle, or several, is to be found in a mature condition in an inflorescence. The matter appears to

[50] Corry, op. cit. p. 175. 1884.

relate to nutrition rather than fertilization. Moore[51] attributes the collapse of pods in *Asclepias syriaca*, in part at least, to competition for food between the endosperm and the adjacent maternal tissue in the ovules.

The follicles in *Sarcostemma* are narrowly fusiform to obclavate, except for S. *pannosum* and the Argentine race of S. *clausum*, where they are inflated at the base. According to Teodoro Meyer[52], the corky, inflated follicles of this race of S. *clausum* are adapted for floating.

The seeds are unequally biconvex or complanate. Usually the dorsal side is more or less rugose, and the flatter, ventral side bearing the obscure raphe, minutely papillate. The margin is flattened and may be serrate at the chalazal end. The white or yellowish coma is produced at the micropylar end of the seed. In the Asclepiadaceae, the coma arises from the rim of the micropyle on the side toward the funicle and does not encircle the micropyle.[53] The presumptive papillae scarcely are apparent in the flower at anthesis, but after fertilization they undergo remarkably rapid growth to produce the apparatus for wind transport so characteristic of the family.

There are few reliable taxonomic characters in the fruit and seeds. It is only with considerable experience with a genus that one can safely identify fruiting specimens in the Asclepiadaceae.

Geography

While particular geographic problems will be discussed under the species to which they pertain, it may be of interest to present a general picture of the distribution of *Sarcostemma*.

The subgenus Ceramanthus includes species from southwestern United States to northern Argentina. The center of diversity is in Mexico, from whence the species extend into more or less xeric habitats, at low to moderate altitudes, to the north and south. In northern Mexico and in the southwestern United States, the plants inhabit dry, sandy washes or arroyos, and they show morphological reduction in a number of aspects. The few specimens which have been collected from less restrictive habitats, such as drainage ditches, have much larger flowers and leaves. In southern Mexico and in South America, the plants attain greater size, although they still prefer such drier areas as savannas or forest margins. On the *llanos* of Argentina, the halophytic S. *gracile* again shows reduction.

Sarcostemma clausum has the widest range of the species in this subgenus, extending from Sonora and Florida to northern Argentina. It has developed numerous local variants of pubescence, leaf shape, and peduncle length, which have not been recognized taxonomically. It is unfortunate that the paucity of specimens from South America does not permit a detailed analysis of this interesting species.

[51] Moore, Raymond J. Investigations on rubber-bearing plants. III. Development of normal and aborting seeds in *Asclepias syriaca* L. Can. Jour. Res. 24C:64. 1946.

[52] Meyer, T. Los generos "Funastrum" y "Philibertia." Lilloa 9:430. 1943.

[53] Hildebrand, F. Über die Entwicklung der haarigen Anhänge an Pflanzensamen. Bot. Zeit. 30:233, 257. 1872.

The species of the subgenus Oxystelma are divided among three sections, one of which is limited to the Old World. In the New World, the species of § Philibertia and § Pentacyphus occur in Andean South America, being centered, with respect to diversity, in northern Argentina and adjacent Bolivia. Like the species of subg. Ceramanthus in preferring more or less arid habitats, the American oxystelmas occur at moderate to high altitudes.

The single Old World species of subg. Oxystelma is *Sarcostemma* (§ Euoxystelma) *esculentum*, which is a weedy plant ranging from Egypt through India to the islands of the East Indies. Apparently it grows in forest clearings and margins, especially along water courses. Its distribution possibly has been affected by man, for it occasionally is cultivated for its fruit and often is found in flower gardens because of its striking flowers.

The leafless sarcostemmas of subg. Eusarcostemma range from southernmost Africa and Madagascar, up the eastern coast of Africa to India, the East Indies, and Australia. They are plants of very dry, rocky or sandy areas, and their adaptation to these xeric habitats is manifest in the scale-like leaves and succulent, photosynthetic stems.

There are thus four main groupings of the species of *Sarcostemma*, which coincide in part with and substantiate the natural subgeneric groups recognized here. They suggest, also, that the genus itself is, in a sense, unnatural in that it includes several distinct evolutionary entities. This idea will be discussed further in the section on relationships. These major geographic and systematic groups include, then, the predominantly Mexican and Central American subg. Ceramanthus, the Andean subg. Oxystelma, § Philibertia and § Pentacyphus, and the two superposed Afro-Asian subg. Oxystelma, § Euoxystelma and subg. Eusarcostemma (which do not appear to be closely related).

Although the systematics of the Old World forms is confused thoroughly at the specific level, it is possible to make certain comparisons between the subgenera and sections with respect to the number of species and degree of specialization and endemism which is apparent in each.

The subgenus Ceramanthus is the largest group, comprising fourteen closely related species which have been arranged taxonomically only in morphological series. Of these species, one is widespread, ten are of moderate extension, and three are rather strict endemics. Nearly all but the endemic species show one or several infraspecific groups at various levels of differentiation.

In the subgenus Oxystelma, there are nine species which break apart sharply into sections. In the Western Hemisphere, § Philibertia comprises five species which are fairly localized in their distribution; one species, however, is endemic to a small area in Argentina; another extends from southern Bolivia to south-central Argentina. About half of these species have developed infraspecific variants. The two species of § Pentacyphus are very distinct morphologically; again, one is rare, the other of moderate range.

Sarcostemma (§ EUOXYSTELMA) *esculentum* appears to be rather homogeneous throughout its range, differing only in vegetative characters and details of the fruit, and showing no tendency toward the striking floral variation of the New World forms. In this sense, it is comparable to *S.* (CERAMANTHUS) *clausum*, although it is the only species in the section and is very complex florally.

While it cannot be stated exactly to what degree the species of subg. EUSARCOSTEMMA are localized, it would appear that most have relatively wide distributions. Yet these species again seem to be very much alike in floral structure across their distribution from Africa to Asia.

These differences in degree of homogeneity and restriction to particular areas are rather interesting. They suggest that, of the three subgenera, CERAMANTHUS is undergoing the most rapid evolution at present. Subgenus OXYSTELMA appears to have achieved greater stability in certain respects, but in the New World is still becoming more diversified. On the other hand, the rather meagre evidence from the Old World seems to indicate that the species there are not actively developing new forms or are specializing along different lines.

RELATIONSHIPS

It has been mentioned that the taxonomy of the Asclepiadaceae is in a very confused state. Until a general system has been developed for the family, discussions of relationships and phylogeny scarcely will be intelligible. At present, the family is split into the Cynanchoideae, comprising the typical Asclepiadaceae with pollinia, and the much smaller, exclusively Old World, Periplocoideae, in which true pollinia are lacking. These divisions are discontinuous and undoubtedly natural, but the smaller subdivisions are less satisfactory.

The Cynanchoideae have been divided into four tribes: Asclepiadeae, Secamoneae, Tylophoreae, and Gonolobeae.[54] The Secamoneae, which have 4-locular anthers and occur only in the Old World, need not concern us. Woodson[55], after critical study of the other three tribes in North America, has presented a key to the tribes, the novel feature of which is his use of the sculptured, partially sterile pollinia of the Gonolobeae as a major character. The Asclepiadeae and Tylophoreae are distinguished, as is customary, by the position of the pollinia, i. e. whether pendulous or erect, respectively. Although the Gonolobeae have been defined unmistakeably, the distinction between the two tribes with uniformly fertile (with but rare exceptions), unsculptured pollinia seems not yet sufficiently decisive.

Sarcostemma is referred to the tribe Asclepiadeae of the Cynanchoideae. Since the genera which have been placed in synonymy have been drawn from three of Schumann's subtribes, no attempt will be made to allocate the genus to one of his artificial subdivisions. For the present, it must suffice to point out the morphological relationships of the genus.

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[54] Schumann, op. cit. 1897.
[55] Woodson, op. cit. 1941.

Sarcostemma is closest to *Cynanchum* and *Blepharodon*. The coronal appendages of *Cynanchum* usually are laminate and variously lobed or united. There are species, however, in which the corona lobes in life are quite fleshy so that little modification need be imagined to produce an inflated structure comparable to that of *Sarcostemma*. In those forms, however, the anther wings usually are not turned at an angle to the plane of the anther, nor are the pollen sacs usually apparent on the back of the anthers, as is characteristic of *Sarcostemma*.

The genus *Blepharodon* consists of two groups of species. Those typified by *B. nitidus* have corona segments which may be considered to consist of two radially arranged, laminate lobes partially fused by their margins. The second group, of which *B. mucronatum* is an example, has semi-vesicular corona segments which are open apically or closed by a thin membrane. In detail they are similar to those of the first group. Thus, from the standpoint of the corona, *Blepharodon* might be considered more or less transitional between *Cynanchum* and *Sarcostemma*. From the latter it differs in the saccate or vesicular corona segments, the anther wings usually in the same plane as the anther, and the very short caudicles bearing pyramidal pollinium-sacs. These same characters, however, together with details of the androecium and stigma-head, preclude relating the genera in linear sequence. Neither *Cynanchum* nor *Blepharodon* has a corona ring, though occasionally there are structures in each which might be mistaken for such.

I am not yet able to discuss satisfactorily the evolutionary relationships of the species of *Sarcostemma*, except for the statements made in connection with the section on geographical distribution and the discussion of certain minor trends which will be noted under the individual species. The plants apparently all have evolved toward the xerophytic type, for the most complex florally are the most specialized in this respect. In most cases the species have developed mechanical isolating mechanisms based on floral structure. Reasoning by analogy with the Asclepiadaceae which have been studied cytologically, it does not seem likely that polyploidy has played a significant role in the evolution of the genus.

I believe that the three subgenera and several sections recognized here are reasonably natural groups encompassing closely related species. Their aggregation into a broadly inclusive and arbitrary genus perhaps needs some explanation. While it may be our ideal to have a taxonomic system which expresses precisely the phylogeny of the organisms involved, the facts of evolution all too often do not permit this. Thus while species in the Asclepiadaceae generally are very well-marked, genera are extremely difficult to delimit. When the entire range of variation is considered, certain centers of variation can be perceived, and it would seem that these should be the basis for building up of genera by accretion, as it were. This has not been done, however, and the description of many small, ill-correlated genera has created a chaotic situation. Because of the nature of taxonomy and nomenclature, the only remedy is the establishment of inclusive, even if somewhat arbitrary, genera which will integrate these smaller groups into a usable system.

Materials

Specimens from the herbaria of the following institutions have been studied:

Chicago Museum of Natural History.
Dudley Herbarium of Stanford University.
Gray Herbarium of Harvard University.
University of Cambridge.
Missouri Botanical Garden.
Museum National de l'Histoire Naturelle, Paris.
Naturhistoriska Riksmuseet, Stockholm.
New York Botanical Garden.
Royal Botanic Gardens, Kew.
United States National Herbarium.
University of California, Berkeley.

I am indebted to the curators of these herbaria for the loan of this material, including many valuable types. I also wish to thank the staff of the Missouri Botanical Garden and its director, Dr. G. T. Moore, for the use of the library and herbarium facilities. To Dr. R. E. Woodson, Jr., I am especially grateful for his generous advice and invaluable constructive criticism.

For species in the United States, only one specimen per county has been cited. For those in other countries, nearly complete citations have been given. Data on habitat and blooming and fruiting time are summarized in the discussion following the description. The distribution maps include all specimens examined which could be located precisely. However, a complete list of all the plants examined is provided in the Index to Exsiccatae, together with the number of the species to which they are referred in this account.

Taxonomy

SARCOSTEMMA R. Brown, in Mem. Wern. Soc. 1:50. 1809, emend. R. Holm.

Oxystelma R. Br. loc. cit. 40. 1809.
Philibertia HBK. Nov. Gen. et Sp. Pl. 3:195. 1819.
Pentagonium Schauer, in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.
Lugonia Wedd. Chlor. And. 2:49. 1857.
Zosima Phil. Sert. Mend. Alt. 29. 1871, non Hoffm.
Funastrum Fourn. in Ann. Sci. Nat. Bot. VI, 14:388. 1882.
Cystostemma Fourn. in Mart. Fl. Bras. 6^4:204. 1885.
Philibertella Vail, in Bull. Torr. Bot. Club 24:305. 1897.
Ceramanthus (Kunze) Malme, in Ark. Bot. 4^{14}:2. 1905, nec Hassk. nec Hook. f. (based on *Sarcostemma* subg. CERAMANTHUS Kunze in Linnaea 20:26. 1847.)
Pentacyphus Schltr. in Engl. Bot. Jahrb. 37:605. 1906.
Tetraphysa Schltr. loc. cit. 616. 1906.

Suffrutescent, dextrorsely twining or trailing vines, rarely semi-erect, the stem variously little- or much-branched. Leaves usually laminate, sometimes reduced to scales, usually with one or more glands on the ventral surface of the midrib at the base; stipules minute. Inflorescences extra-axillary, cymose, racemiform to umbelliform, 1- to 30-flowered; peduncle present or absent. Calyx 5-lobed nearly to

the base which is adnate to the corolla, usually with 1 to many alternate or indefinitely distributed squamellae within. Corolla 5-lobed, rotate-subcampanulate, campanulate, or salverform. Stamens 5, the filaments coherent to form a column (rarely obsolete), usually produced at their insertion upon the corolla to form a patelliform corona ring often completely adnate to the corolla or to the filaments directly below the anthers, each filament bearing an inflated, vesicular segment (corona vesicle) directly below the anther; anthers 2-celled, the thecae apparent dorsally, the alae usually at 45° to the anther, the membranous dorsal appendage ovate to deltoid; pollinium-sacs oblongoid-cylindrical to clavate, nearly uniformly rounded or flattened, uniformly fertile (rarely with a small sterile region at the attachment of the caudicle), the corpusculum sagittate to ellipsoid, the slender caudicles exceeding the corpusculum in length, rarely very short. Carpels 2, somewhat subinferior, free towards the base, prolonged above into relatively conspicuous styles which unite to form a convex to 2-apiculate stigma-head. Follicle fusiform to obclavate; seeds unequally biconvex or flattened, with a micropylar coma.

Type species: *Sarcostemma viminale* (L.) R. Br.

KEY TO THE SUBGENERA

A. Stems never succulent; leaves laminate; inflorescence racemiform to umbelliform, the peduncle usually manifest; corolla rotate-subcampanulate, campanulate, or salverform; vesicles of the corona ovoid or obovoid to oblongoid or spheriod, ring of the corona free or adnate to the column directly below the anthers.
  B. Corolla rotate-subcampanulate or salverform; ring of the corona free from the corolla, porrect (lacking in S. *flavum*); inflorescence corymbiform to umbelliform, 4- to 30-flowered. Species of the Western Hemisphere ..... Subgenus I. CERAMANTHUS (p. 506)
  BB. Corolla campanulate; ring of the corona adnate to the corolla or more or less obsolete; inflorescence racemiform or umbelliform, 1- to 10-flowered. Species of the Eastern and Western Hemispheres. ..... Subgenus II. OXYSTELMA (p. 537)
AA. Stems succulent, or woody below; leaves scale-like throughout; inflorescence subumbelliform, the peduncle obsolete; corolla rotate-subcampanulate; vesicles of the corona ovoid, ring of the corona adnate to the filaments. Species of the Eastern Hemisphere..... Subgenus III. EUSARCOSTEMMA (p. 482)

Subgenus I. CERAMANTHUS Kunze, in Linnaea 20:26. 1847.

Philibertia acc. to Benth. in Benth. & Hook. Gen. Pl. 2:733. 1876, non HBK.
Funastrum Fourn. in Ann. Sci. Nat. Bot. VI, 14:388. 1882.
Cystostemma Fourn. in Mart. Fl. Bras. 6^4:204. 1885.
Philibertella Vail, in Bull. Torr. Bot. Club 24:305. 1897.
Ceramanthus (Kunze) Malme, in Ark. Bot. 4^{14}:2. 1905, nec Hassk. nec Hook. f.

Leaves laminate, rarely caducous or reduced; inflorescence corymbiform to umbelliform; corolla rotate-subcampanulate or salverform; ring of the corona usually pronounced (lacking in S. *flavum*).

Type species: *Sarcostemma elegans* Decne.

A closely knit group of species inhabiting drier regions of tropical and temperate America. The keys have been written so that flowers need not be studied critically for identification. Examination of the dried flowers with a hand lens often will provide a reassuring check on vegetative characters, however. All the

species recognized here differ from one another in many aspects of floral structure, but these differences often are difficult to describe adequately. Recourse may be had to the drawings of the gynostegia which have been made to show a condition typical for each species.

KEY TO THE SERIES

A. Ring of the corona present. Plants of North and South America.
  B. Inflorescence lateral to the main axis or lateral branch.
    C. Inflorescence corymbiform, obviously compound, the peduncle not equalling the subjacent internode in thickness; leaves usually densely white-tomentose beneath. Plants of Mexico.....Series 1. PANNOSA (Sp. 1)
    CC. Inflorescence umbelliform, the pedicels all inserted at nearly the same point; leaves never densely white-tomentose beneath.
      D. Peduncle equalling or exceeding the subjacent internode in thickness or lacking (when lacking, leaves obtuse to cuneate at the base), frequently bearing two catenulate cymes.....Series 2. CLAUSA (Spp. 2–3)
      DD. Peduncle not equalling the subjacent internode in thickness, or lacking (when lacking, leaves cordate), usually bearing but one cyme. .....Series 3. CYNANCHOIDES (Spp. 4–12)
  BB. Inflorescence terminal to the main axis or lateral branch, the peduncle not equalling the subjacent internode in thickness, or lacking. Plants of the Galapagos Islands.....Series 4. ANGUSTISSIMA (Sp. 13)
AA. Ring of the corona lacking. Plants of Argentina, Brazil and Uruguay. .....Series 5. FLAVA (Sp. 14)

Series 1. PANNOSA R. Holm, ser. nov.

Inflorescentia ut videtur lateralis corymbiformis certe composita, pedunculo quam internodio subjacenti angustiore.

Type species: *Sarcostemma pannosum* Decne.

A monotypic series which contains the presumably primitive species of the subgenus. The obviously compound inflorescence characterizes the series.

1. SARCOSTEMMA PANNOSUM Decne. in DC. Prodr. 8:540. 1844.

Sarcostemma rotundifolium Decne. loc. cit. 1844, ex char. (T.: *Mairet de la Chaux de Fond in Herb. DC.*).
Philibertia pannosa (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:320. 1881.
Philibertia rotundifolia (Decne.) Hemsl. loc. cit. 1881.
Philibertia Pavoni Hemsl. loc. cit. 319. 1881. (T.: *Ghiesbreght 200 in Herb. Kew.*!).
Philibertia tomentella T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:90. 1900. (T.: *Brandegee 361 in Herb. Univ. Calif.*!).
Funastrum pannosum (Decne.) Schltr. in Fedde's Repert. 13:286. 1915.
Funastrum rotundifolium (Decne.) Schltr. loc. cit. 287. 1915.
Funastrum Pavoni (Hemsl.) Schltr. loc. cit. 286. 1915.
Funastrum tomentellum (Brandeg.) Schltr. loc. cit. 287. 1915.
Sarcostemma tomentellum (Brandeg.) Woods. in Ann. Mo. Bot. Gard. 28:217. 1941.

Stems twining, minutely pilosulose; lateral branches normally several. Leaves oblanceolate to obovate-elliptic, acuminate to mucronate, broadly and more or less obscurely cordate, 3.5–9.0 cm. long, 1.5–5.0 cm. wide, subcoriaceous, pilosulose above, densely white-tomentose beneath, with one or more glands on the midrib at the base; petiole 1–3 cm. long. Inflorescences corymbiform, 9- to 30-flowered; peduncle 3–7 cm. long, not equalling the subjacent internode in thickness, minutely pilosulose; bracts linear, minute; pedicels 2.0–3.5 cm. long, minutely pilosulose.

Calyx lobes narrowly ovate, 2.5–4.0 mm. long, pilosulose on both surfaces; squamellae absent or solitary. Corolla rotate-subcampanulate, white or cream-colored, the tube 1.5 mm. long, the lobes ovate, acuminate, 7–10 mm. long, pilosulose without, more or less puberulous-papillate within. Gynostegium 4 mm. high, the column 1.5 mm. long. Anthers 2 mm. long, the apical appendage ovate-suborbicular, the pollinium-sacs oblongoid-cylindrical, 1.2 mm. long with sagittate corpusculum; ring of the corona thin, revolute; vesicles of the corona obovoid, 2.5 mm. long. Ovaries 2.5 mm. long, the styles sericeous; stigma-head conical, 2-apiculate. Follicles broadly fusiform-obclavate, 5–7 cm. long, 2.0–2.5 cm. thick, puberulent; seeds unequally biconvex, 2.5–3.0 mm. long, 1.5–2.0 mm. wide, rufescent, rugose dorsally, papillate ventrally; coma about 2 cm. long.

An attractive species, well-marked by the white tomentum on the under-side of the leaf. In the very rare instances when this pubescence is not dense, the inflated follicle and compounding of the inflorescence are diagnostic. At least one segregate species has been based on a lack of undulation of the leaves *(P. Pavoni)*. However, I have found that on a single plant of *S. pannosum* in cultivation, the leaves may be plane or undulate. A similar situation obtains in *S. crispum*.

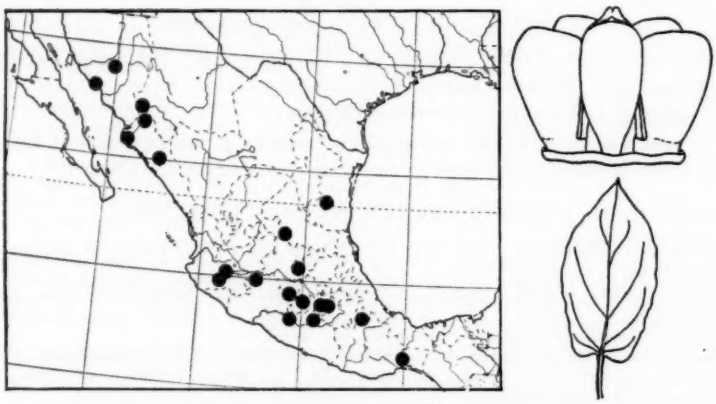

Fig. 5. Distribution, gynostegium, and leaf of *S. pannosum*.

Sarcostemma pannosum is endemic to Mexico, where it grows on grassy or rocky slopes from 500 to 6000 feet. It has been collected in flower from July 17 to November 19; fruit has been found from September 22 to November 13.

MEXICO. CHIHUAHUA: Guasarémos, Río Mayo, *Gentry 2369*. DURANGO: loc. unknown, *Rose 2310*. GUERRERO: Pungarabato, Cayuca, *Hinton 6470*; Sierra Madre del Sur, Adama, Temisco, *Mexia 8861*; Placeres, Mina, *Hinton 10528*; Puerta de Oro, Mina, *Hinton 9175*; mts. near Iguala, *Pringle 13593*. JALISCO: Tuxcacuesco, *E. Anderson s. n.*; Río Blanco, *E. Palmer 340*; Sacoaco, *M. E. Jones 319*. MEXICO: Temascáltepec, Vigas, *Hinton 1191*. MICHOACÁN: Monteleón, *Pringle 11028*; near Zamora, *Schery 182*; Tuzantla, Tiquicheo, Zitácuaro, *Hinton 13077*. MORELOS: near Yuatepec, *Rose, Painter & Rose 8585*; Cuernavaca, *Kenoyer C220*, *M. Martínez 150/02*. NAYARIT: Tepic, Los Bules,

Goldsmith 170. OAXACA: San Gerónimo, *Purpus 7180;* Oacalco, *Nagel 8086.* PUEBLA: Coxcatlán, *Purpus 4118.* QUERÉTARO: loc. unknown, *Agniel 14;* near Querétaro, *Rose & Rose 11152;* Querétaro, *Kuntze 23448.* SAN LUIS POTOSÍ: Las Canoas, *Pringle 3227.* SINALOA: Culiacán, *E. Palmer 1492;* El Brasil, Rancho Tasajera, Choix, *Montes & Salazar 881;* Topolobambo, *E. Palmer 185;* near Labradas, *Ferris & Mexia 5247.* SONORA: 9 miles NE of Colorado, between Colorado & Mazatlán, *Wiggins & Rollins 328;* Guaymas, *E. Palmer 195.* TAMAULIPAS: near Victoria, *Palmer 497.*

Series 2. CLAUSA R. Holm, ser. nov.

Inflorescentia ut videtur lateralis umbelliformis saepe cymis catenulatis duobus, pedunculo internodium subjacens crassitudine aequante vel excedente (interdum obsoleto).

Type species: *Sarcostemma clausum* (Jacq.) R. & S.

This series includes two species which share the character of having peduncles as thick as, or thicker than the subjacent internode. It is also quite common to find two umbelliform clusters of flowers upon the same peduncle, one terminal, the other lateral.

KEY TO THE SPECIES

a. Corolla salverform, the tube definitely constricted; ovaries glabrous throughout; plants more or less glaucous throughout ..... 2. *S. glaucum*
aa. Corolla rotate-subcampanulate, the tube not definitely constricted; ovaries sericeous throughout or with densely sericeous styles; plants glabrescent to sericeous ..... 3. *S. clausum*

2. SARCOSTEMMA GLAUCUM HBK. Nov. Gen. et Sp. Pl. 3:194. 1819, ex char. (T.: *Humboldt & Bonpland s. n. in Herb. Paris.*).

Funastrum glaucum (HBK). Schltr. in Fedde's Repert. 13:285. 1915.
Philibertella ovalifolia Rusby, Descr. So. Am. Pl. 94. 1915. (T.: *H. H. Smith 1683 in Herb. N. Y. Bot. Gard.*!).
Funastrum ovalifolium (Rusby) Killip, in Jour. Wash. Acad. Sci. 21:351. 1931.

Stems twining, gray-green, glabrous; lateral branches normally few. Leaves narrowly elliptic, oblong to ovate, acute, cuneate to obtuse, 5.0–7.5 cm. long, 0.5–3.0 cm. wide, subcoriaceous, revolute when dried, glaucous, glabrous on both surfaces, with one or more glands on the midrib at the base; petiole 0.3–0.5 cm. long. Inflorescences umbelliform, 18- to 35-flowered; peduncle 0–7 cm. long, equalling the subjacent internode in thickness, often bearing two catenulate cymes, glabrous; bracts linear, minute; pedicels 1–2 cm. long, glabrous. Calyx lobes ovate, 1.5 mm. long, glabrate on both surfaces, ciliolate; squamellae absent. Corolla salverform, white, the tube 2 mm. long, constricted, the lobes ovate, obtuse, 4–6 mm. long, puberulous-papillate on both surfaces, ciliolate. Gynostegium 2 mm. high, the column about 0.5–1.0 mm. long. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs oblongoid, somewhat flattened, 0.75 mm. long, with ellipsoid-sagittate corpusculum; ring of the corona prominent, revolute, adnate to the base of the corona vesicles; vesicles of the corona ovoid, pointed at the tip, 1.5–2.0 mm. long. Ovaries 3 mm. long, glabrous; stigma-head conical, obscurely 2-fid. Follicles narrowly obclavate-fusiform, 8.5 cm. long, 1 cm. thick,

glabrous; seeds flattened, 6 mm. long, 4 mm. wide, minutely papillate on both surfaces, the margin thin and serrate apically; coma about 2.5 cm. long.

This species often is confused with *S. clausum*, but although the two are alike superficially, there are a number of characters to separate them. One of the best is the fact that the corolla tube is constricted in *S. glaucum*, while the flowers are somewhat smaller and more abundantly produced. As the specific name suggests, *S. glaucum* has a characteristic glaucous aspect throughout. The doubled inflorescence also is more common in this species, where the peduncle sometimes is absent.

Philibertella ovalifolia Rusby was described for a variant with leaves wider than those of the typical form, but the two sorts occur in the same area and merge with one another. Although *S. glaucum* appears to be fairly common, only one specimen with fruit has been seen.

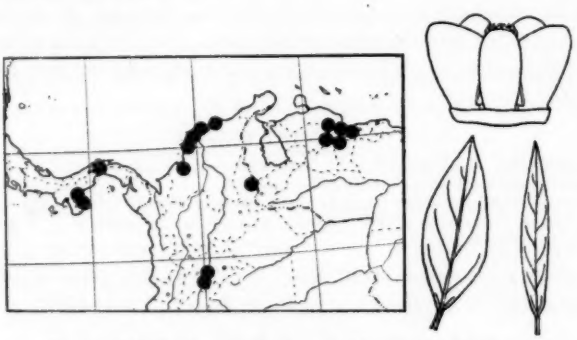

Fig. 6. Distribution, gynostegium, and leaves of *S. glaucum*.

Sarcostemma glaucum has been collected in Panama, Venezuela, and Colombia, where it grows along the coast, both in marshy and arid thickets or forest margins. The maximum recorded altitude attained by the species is 2500 feet, but it appears to be more common near sea level. Flowering specimens are dated from July 19 to March 6.

PANAMA. COCLÉ: Aguadulce, *Pittier 4977*. HERRERA: near Chitré, *Allen 1090*. PANAMA: Juan Díaz, *Standley 30510*.

COLOMBIA. ATLÁNTICO: Ponedera, *Dugand & Jaramillo 2750*; between Palmar de Varela & Pondedera, *Dugand 3658*; Puerto Giraldo, *Dugand & Jaramillo 4187*. BOLIVAR: Cartagena, *E. Martínez 83, Heriberto 288*; Barranquilla, *Elias 441, Dugand 102*; Los Volcánes, near Turbaco, *Killip & Smith 21111, 14323*; S of Mawatoca, *H. H. Smith 2779*; Sincelejo, *Pennell 4058*. CUNDINAMARCA: Girardot, *Rusby & Pennell 76*; Hacienda El Cucharo, between Tocaima & Pubenza, *Killip, Dugand & Jaramillo 38922*. HUILA: quebrada de Ângeles to Río Cabrera, *Rusby & Pennell 342*. MAGDALENA: Santa Marta, *H. H. Smith 1682, 2524, Killip & Smith 21105*. SANTANDER DEL NORTE: Cúcuta, *Killip & Smith 20999*.

VENEZUELA. ARAGUA: La Trinidad de Maracay, *Pittier 5783*. CARABOBO: near Valencia, *Pittier 9429*; near Trincheras, near Valencia, *Pittier 7653*. LARA: Barquisimeto, *Santiago 60*. PORTUGUESA: near Acarigua, *L. Williams 12460*. ZULIA: near Perijá, *Tejera 201, 225*.

PERU. data incomplete, *Maclean s. n.*

3. SARCOSTEMMA CLAUSUM (Jacq.) Roem. & Schult. Syst. Veg. 6:116. 1820.

Cynanchum clausum Jacq. Select. Stirp. Amer. 1:87, *t. 60.* 1763.
Asclepias viminalis Sw. Prodr. 53. 1788.
Sarcostemma Brownei G. F. Meyer, Prim. Fl. Esseq. 139. 1818.
Sarcostemma cumanense HBK. Nov. Gen. et Sp. Pl. 3:195. 1819, ex char. (T.: *Humboldt & Bonpland s. n. in Herb. Paris.*).
Sarcostemma pubescens HBK. loc. cit. 194. 1819, ex char. (T.: *Humboldt & Bonpland s. n. in Herb. Paris.*).
Sarcostemma Swartzianum Schult. Syst. Veg. 6:116. 1820.
Sarcostemma lineare Spreng. Neue Entd. 3:35. 1822, non Decne.
Sarcostemma bonariense Hook. & Arn. in Hook. Lond. Jour. Bot. 1:296. 1834, ex char. (T.: *Tweedie s. n. in Herb. Kew.*).
Sarcostemma apiculatum Decne. in DC. Prodr. 8:539. 1844, ex char. (T.: *Gardner 819 in Herb. Delessert*).
Sarcostemma crassifolium Decne. loc. cit. 540. 1844, ex char. (T.: *Galeotti 1529 in Herb. Paris.*).
Sarcostemma Dombeyanum Decne. loc. cit. 539. 1844. (T.: *Dombey s.n. in Herb. Paris!*).
Sarcostemma riparium Decne. loc. cit. 540. 1844, ex char. (T.: *in Herb. Paris.*).
Philibertia viminalis (Sw.) A. Gray, in Proc. Amer. Acad. 12:64. 1877.
Philibertia crassifolia (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.
Philibertia cumanensis (HBK.) Hemsl. loc. cit. 1881.
Sarcostemma barbatum Mart. ex Fourn. in Mart. Fl. Bras. 6^4:235. 1885, ex char. (T.: *Martius s. n.*).
Sarcostemma bifidum Fourn. loc. cit. 234. 1885, ex char. (T.: *Mikan I in Herb. Vindobon.*).
Sarcostemma cuspidatum Fourn. loc. cit. 233. 1885, ex char. (T.: *Poeppig 2923 in Herb. Vindobon.*).
Sarcostemma Gardneri Fourn. loc. cit. 1885, ex char. (T.: *Gardner 1357*).
Sarcostemma pallidum Fourn. loc. cit. 235. 1885, ex char. (T.: *St. Hilaire Cat. C^2 1489*).
Sarcostemma pedunculatum Fourn. loc. cit. 1885, ex char. (T.: *Glaziou 8168 in Herb. Paris.*).
Sarcostemma Schottii Fourn. loc. cit. 234. 1885, ex char. (T.: *Pohl & Schott 5381 in Herb. Vindobon.*).
Philibertia Palmeri A. Gray, in Proc. Amer. Acad. 21:394. 1886. (T.: *Palmer 5 in Herb. Gray!*).
Philibertia clausa (Jacq.) K. Schum. in E. & P. Nat. Pflanzenfam. 4^2:229. 1895.
Philibertia Gardneri (Fourn.) K. Schum. loc. cit. 1895.
Philibertella clausa (Jacq.) Vail, in Bull. Torr. Bot. Club 24:306. 1897.
Philibertella crassifolia (Decne.) Vail, loc. cit. 1897.
Philibertella cumanensis (HBK.) Vail, loc. cit. 1897.
Philibertella Palmeri Vail, loc. cit. 1897.
Sarcostemma Glaziovii K. Schum. in Engl. Bot. Jahrb. 25, Beibl. 60:19. 1898, ex char. (T.: *Glaziou 21744 in Herb. Berol.*).
Philibertia bonariensis (H. & A.) Malme, in Sv. Vet. Akad. Afh. 34:23. 1900.
Philibertia cuspidata (Fourn.) Malme, loc cit. 24. 1900.
Philibertia riparia (Decne.) Malme, in Bih. Sv. Akad. Vet. 27:7. 1901.
Philibertella lasiantha Schltr. in Engl. Bot. Jahrb. 37:607. 1906, ex char. (T.: *Eggers 14547 in Herb. Berol.*).
Philibertella pallida (Fourn.) Schltr. loc. cit. 1906.
Philibertella pedunculata (Fourn.) Schltr. loc. cit. 1906.
Cynanchum mexicanum T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:380. 1913. (T.: *Purpus 6017 in Herb. Univ. Calif.*!).
Philibertella riparia (Decne.) Stuntz, Invent., U. S. Bur. Pl. Ind. 31:87. 1914.
Funastrum apiculatum (Decne.) Schltr. in Fedde's Repert. 13:283. 1915.
Funastrum barbatum (Mart.) Schltr. loc. cit. 1915.

Funastrum bonariense (H. & A.) Schltr. loc. cit. 1915.
Funastrum clausum (Jacq.) Schltr. loc. cit. 1915.
Funastrum crassifolium (Decne.) Schltr. loc. cit. 1915.
Funastrum cumanense (HBK.) Schltr. loc. cit. 1915.
Funastrum cuspidatum (Fourn.) Schltr. loc. cit. 1915.
Funastrum Dombeyanum (Decne.) Schltr. loc. cit. 1915.
Funastrum Gardneri (Fourn.) Schltr. loc. cit. 1915.
Funastrum Glaziovii (K. Sch.) Schltr. loc. cit. 1915.
Funastrum lasianthum Schltr. loc. cit. 1915.
Funastrum pallidum (Fourn.) Schltr. loc. cit. 1915.
Funastrum Palmeri (A. Gray) Schltr. loc. cit. 1915.
Funastrum pedunculatum (Fourn.) Schltr. loc. cit. 1915.
Funastrum pubescens (HBK). Schltr. loc. cit. 1915.
Funastrum riparium (Decne.) Schltr. loc. cit. 1915.
Funastrum Schottii (Fourn.) Schltr. loc. cit. 287. 1915.
Funastrum fragile Rusby, in Mem. N. Y. Bot. Gard. 7:332. 1927. (T.: *White 2088 in Herb. N. Y. Bot. Gard.*!).
Funastrum lanceolatum Rusby, loc. cit. 1927. (T.: *M. Cardenas 2 in Herb. N. Y. Bot. Gard.*!).
Funastrum Seibertii Woods. in Ann. Mo. Bot. Gard. 24:199. 1937. (T.: *Seibert 637 in Herb. Mo. Bot. Gard.*!).

Stems twining or trailing, gray-green, glabrous, the nodes densely white-pubescent; lateral branches normally few. Leaves frequently caducous, elliptic to oval, rarely much reduced, acuminate to mucronate, obtuse to shallowly cordate, 2–5 cm. long, 0.5–2.5 cm. wide, membranaceous to subcoriaceous, glabrate to sericeous above and beneath, with one or more glands on the midrib at the base; petiole 0.2–0.6 cm. long. Inflorescences umbelliform, rarely with two catenulate cymes, 7- to 15-flowered; peduncle stout, usually equalling the subjacent internode in thickness, 3.5–6.0 cm. long, glabrate to sericeous; bracts linear, minute; pedicels 1.5–2.5 cm. long, glabrate to puberulent. Calyx lobes ovate, 3–4 mm. long, densely puberulent without, glabrate within; squamellae alternate, paired or solitary. Corolla rotate-subcampanulate, pale greenish yellow to white, the tube 2.5 mm. long, not definitely constricted, the lobes ovate-elliptic, acute, 6–9 mm. long, densely puberulent without, glabrate to minutely puberulent within, ciliolate. Gynostegium 3 mm. high, the column short, about 0.5 mm. long. Anthers 1.5 mm. long, the apical appendage reniform to orbicular, the pollinium-sacs cylindrical-oblongoid, 1.8 mm. long, with sagittate corpusculum; ring of the corona prominent, revolute, adnate to the base of the corona vesicles; vesicles of the corona ovoid, pointed at the tip, 2.5 mm. long. Ovaries 2.5 mm. long, the styles sericeous, rarely sericeous throughout; stigma-head convex, with a short 2-fid apiculation. Follicles obclavate, attenuate, 5.0–8.5 cm. long, 1.2–1.5 cm. thick, puberulent, finely striate; seeds flattened, 4–6 mm. long, 2–3 mm. wide, minutely papillate on both surfaces, the margin thin and serrate apically; coma about 2 cm. long.

A species as bewilderingly variable as *Sarcostemma clausum* poses a serious question for the taxonomist. Although sufficiently common and variable to have developed a phenomenal synonymy, it is not sufficiently abundant in herbaria for analyses of variation to be made. Undoubtedly a species which ranges from southern United States to Argentina, which occupies both hydric and xeric habitats, and

which is insect-pollinated, will differentiate ecologic or geographic populations. Only very limited samples, often of a single plant, of these local groups are available to the botanist. In such a case, one alternative is to describe each specimen which is different in several aspects of morphology as new, in the hope that it eventually will be found to be a valid species. This is what has been done in the past with the majority of the Asclepiadaceae. The other alternative is to recognize that the specimen is slightly different in one, or perhaps several characters, but to refrain from describing it as a species until it can be proven to be a well-defined population which has achieved some measure of isolation from its cogeners.

After studying the some few hundred specimens collected from the entire range of *S. clausum*, I have come to the conclusion that there are essentially no significant differences, although the leaves are quite variable in shape, size, and pubescence, and the peduncles vary in size and thickness. The fact that these vegetative forms tend to occupy certain regions indicates that *S. clausum* probably has differentiated into several subspecific groups. It would be extremely dangerous to attempt to define the limits of such intergrading populations on the basis of a very few examples. I have followed, therefore, the alternative of recognizing only one species which eventually will perhaps be split into smaller groups.

Sarcostemma clausum, generally speaking, inhabits less arid habitats than most of the species of the genus. In Florida, Central America, and eastern South

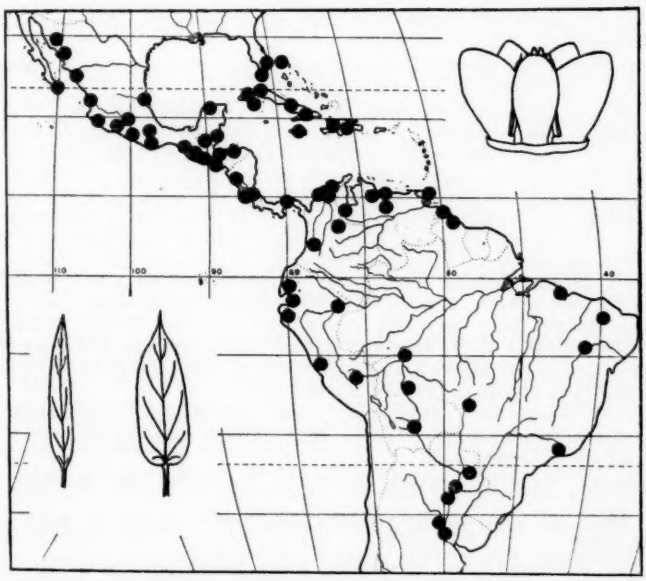

Fig. 7. Leaves, distribution, and gynostegium of *S. clausum*.

America, it is found on wooded slopes or in flood plains, or even growing in several feet of water. In Mexico and northwestern South America, on the other hand, it is commonest in sandy strand areas or savannas. The altitudinal range is from sea level to about 4000 feet. The plant apparently is in flower the year round through most of its range and has been described as "extremely fragrant, covered with masses of white flowers."

UNITED STATES. FLORIDA: DADE CO.: Miami, *Garber 11939*. LEE CO.: Fort Myers, *Hitchcock 207*. MONROE CO.: Fishbone Key, *Seibert 1337*; Big Pine Key, *Killip 3174*; Key West, *Curtiss 5624*; Bahia Honda Key, *Woodson & Schery 119*; Elliot's Key, *Small & Nash s. n.*

MEXICO. BAJA CALIFORNIA SUR: San José del Cabo, *T. S. Brandegee s. n.*; S of San José del Cabo, *Johansen 514*. CHIAPAS: Jalisco, *Purpus 9170*; Escuintla, *Matuda 0699*. CHIHUAHUA: SW Chihuahua, *E. Palmer 5*, type of *P. Palmeri* Gray. COLIMA: Manzanillo, *Ferris 6128*, *Palmer 1002*; Paso del Río, *Emrick 11*. GUERRERO: Baqueta, *Langlassé 508*; Guayameo, Mina, *Hinton 9370*; Actoyac, Galeana, *Hinton 14602*; Vallecitos, Montes de Oca, *Hinton 10607*; Pungarabato, Coyuca, *Hinton 6452*; NW of Acapulco, *Barkley 14103*. JALISCO: Bolaños, *Rose 2912*; Tenacatita Bay, *Elmore 1A23*. MICHOACAN: Coalcomán, Aquila, *Hinton 15833*. MORELOS: near Cuernavaca, *Pringle 7109*; Xochitepec, *Lyonnet 1037*. NAYARIT: Mexcaltitlán, *Mexia 1016*. OAXACA: near Tomellin, *Rose, Painter & Rose 10054*; near Cuicatlán, *E. W. Nelson 1615, 1680, L. C. Smith 249*; Chiltepec, Tuxtepec, *Martínez-Calderón 196*; San Antonio, *C. L. Smith 836*, *Pringle 4849*; Tomellin, *Olssen-Seffer s. n.*; Etla, near Bocas del Ríos, *Seler & Seler 4852*. SINALOA: Culiacán,*T. Brandegee s. n.*; loc. unknown, *Ortega 4230*. SONORA: Hermosillo, *Drouet & Richards 3564*; 23 miles NE Ures, *Shreve 6732*; Río Mayo, *Gentry 2286*; near Batuc, *Wiggins & Rollins 454*; 25 miles from Ures, *Wiggins 7387*. TABASCO: Caño de Curahue, *Rovirosa 32*. TAMAULIPAS: Tampico, *E. Palmer 498*. VERA CRUZ: Pánuco River near Ebano, *Le Sueur 358*; loc. unknown, *Purpus 6017*, type of *C. mexicanum* Brandeg. YUCATAN: Progreso, *Flores 7*.

BRITISH HONDURAS: Corozal District, *Gentle 503, 807*; Honey Camp, *Lundell 517*; Santa Rita, *Gentle 73*; Northern River, *Gentle 883*.

GUATEMALA. ALTA VERAPAZ: Samac, *Johnson 776*; Pancajche, *Johnson 1017*. AMATITLÁN: Amatitlán, *von Tuerckheim 8710*, *J. D. Smith 2778*, *Morales 1136*; Lake Amatitlán, *Kellerman 4359*, *J. D. Smith 1940*. CHIQUIMULA: near Chiquimula, *Standley 73865*. ESCUINTLA: Río Guacalate, *Standley 58204, 60163*; San José, *Standley 63961*, *Hayes s. n.* GUATEMALA: near Lago de Amatitlán, *Standley 89433*. JUTIAPA: near Jutiapa, *Standley 75185*. IZABAL: Boca del Palochi, *J. D. Smith 1734*; NE of San Felipe, *Steyermark 39662*. PETÉN: S of Sayaxche, *Steyermark 46229*. RETALHULEU: near Retalhuleu, *Standley 88251, 88837*. SAN MARCOS: Ocós, *Steyermark 37820*; Río Suchiate, W of Ayutla, *Steyermark 38030*. SOLOLA: S-facing slopes, Volcán Atitlán, *Steyermark 48010*; Santa Barbara, *Shannon 169*. SANTA ROSA: Ríos de los Esclavos, *Heyde & Lux 4001*; Casillos, *Aquilar 303*; Agua Caliente, *Kellerman 7737*. SUCHUTEPEQUEZ: Río Najuala, *Shannon 399*. ZÁCAPA: Baños de Santa Marta, *Standley 73932*; Zácapa, *Deam 154*, *Kellerman 4359*.

EL SALVADOR. AHUACHAPÁN: loc. unknown, *Padilla 115*. SAN SALVADÓR: along road from San Martín to Laguna de Ilopango, *Standley 22589*.

HONDURAS. ATLÁNTIDA: Tela, *Standley 54664*. CORTES: Río Lindo, *Edwards P-683*. SANTA BARBARA: San Pedro Sula, *Thieme 5342*. YORO: near Coyoles, Aguán Valley, *Yuncker, Koepper & Wagner 8122*.

NICARAGUA. GRANADA: Granada, *Grant 903*. MANAGUA: near Managua, *Garnier A128*.

COSTA RICA. SAN JOSÉ: near El Generál, *Skutch 2171*. TALAMANCA: Delta de Turitkub, *Tonduz 8661*.

PANAMA. BOCAS DEL TORO: Changuinola River, *Dunlap 289*. CANAL ZONE: Barro Colorado Island, *Bangham 413*, *Kenoyer 501*, *Shattuck 315*, *1114*, *Brown 155*, *Wilson 66*, *Bailey & Bailey 530*; near Empire, Culebra Cut, *Hunter & Allen 775*. PANAMÁ: swamp

between El Jagua Hunting Club on Río Jagua and El Condor Hill, *Hunter & Allen 482;* near Arenoso, lower Río Trinidád, *Seibert 637.*

CUBA. CAMAGUEY: Cayo Romano, *Shafer 2494;* Cayo Sabinal, Granada, *Shafer 877.* HAVANA: Laguna de Castellano, *P. Wilson 9559;* San Antonio, *Shafer 247.* ORIENTE: Ensenada de Mora, *Britton, Cowell & Shafer 12960;* near Nirua-Nirua, *Britton & Cowell 12719;* Bayamo, *Ekman 7590;* Río Jagua, *Ekman 6653; Wright 1666.* ISLA DE PINOS: Nueva Gerona, *Curtiss s. n.;* Don José, *Blain 104.* LAS VILLAS: Belmonte, Sóledad, Cienfuegos, *Jack 7728, 6856, 5342;* Cienfuegos, Cienquita, *Combs 330;* Ciénaga de Zapata, N of Bahía de Cochinas, *Leon & Soustalot 8497;* Gavilon, vic. Sóledad, *Howard 6298.* PINAR DEL RÍO: near Mendoza, *Shafer 10608;* Laguna Jovera, *Shafer 10983.*

HISPANIOLA. HAITI: near Port au Prince, *Leonard 10092;* near Gros Morne, *Leonard 9934, 9980;* near Jean Rabel, *Leonard & Leonard 12799;* near Étang, *Leonard 3570.*

DOMINICAN REPUBLIC: Barahona, *Fuertes 202, 1260;* S of Monte Cristi, near Río Yaque del Norte, *Howard & Howard 9569.*

JAMAICA: Blue Mts., *Hitchcock s. n.;* Arntully, *Orcutt 3111;* Port Henderson, *Harris & Lawrence C1536;* Hope Bay, *Wight 169;* Kingston, *Brown 379;* below Cinchona, *Maxon & Killip 1043.*

BAHAMA ISLANDS: New Islands, *Britton & Brace 482, 770;* Great Bahama, *Brace 3602, Britton & Millspaugh 2661.*

TRINIDAD: east of Icacos, *Cheesman & Baker 388.*

COLOMBIA. AMAZONAS: Río Putamayo, between Río Igara-Paraná and Río Yaguas, *Schultes 3998.* BOLÍVAR: Calamar, *Killip & Smith 14708;* near Turbaco, *Killip & Smith 14437;* Buenavista, east of Sincé, *Pennell 3981;* near Puerto Colómbia, *Elias 396.* CAUCA: La Manuelita, Palmira, *Pittier 787.* EL VALLE: Espiñol, below Dagua, *Killip & Hazen 11076;* N of Palmire, *Garcia B. 6408;* "La Manuelita," *Pennell & Killip 6191.* HUILA: above Natagaima, *Rusby & Pennell 270.* MAGDALENA: Santa Marta, *H. H. Smith 1681;* Fonseca, *Haught 4387;* 15 miles N of Becerril, *Haught 3694.* SANTANDER: Puerto Wilches, *Killip & Smith 14937.* SANTANDER DEL NORTE: near Sarare, *Cuatrecasas 13258;* near Florida, *Killip & Smith 16176.* TOLIMA: Doima, *Haught 2442;* Mariquita, *Pennell 3632.*

ECUADOR. GUAYAS: Guayaquil, *Mille 961, Asplund 5150.* LOS RÍOS: Río Pita, *Asplund 5588.*

PERU. APURIMAC: Abancay, *Vargas 750.* LIMA: Hacienda Peramango, Río Pativilca Valley, *Seibert 2313;* Chosica, *Macbride & Featherstone 535.* LORETO: Iquitos, Creek Itaya, *Mexia 6482.* PIURA: Huancabamba, Serran, *Stork 11387;* Negritos, *Haught F-49;* Pariñas Valley, *Haught 145, Spruce 6486.* TUMBES: Tumbes, mts. SE Hacienda La Choza, *Weberbauer 7694.*

VENEZUELA. ARAGUA: Maracay, El Limón, *Pittier 10102;* potreros de Las Delicias, *Lasser 860.* DISTRITO FEDERAL: Bajo Cotiza, *Vogl 458;* near Caracas, *Eggers 13121, Pittier 7583.* GUARICO: El Sombrero, *Pittier 13557.* FALCON: Meachiche, *Lasser 186.* MÉRIDA: Tovar, *Fendler 1054.* YARACUY: near Guama, *Pittier 11163.*

BRITISH GUIANA: Vreed-en-Hoop, *Hitchcock 16738;* Morawhanna, *Hitchcock 17511;* Parika, *Hitchcock 16754;* east coast, *Persaud 302.*

SURINAM: *Hostmann 962.*

BRAZIL. CEARÁ: Carupe, *Drouet 2610;* Río de Janeiro, *Glaziou 8168, Dusén 1968.* MATTO GROSSO: Cuyabá, *Malme 3247, Hoehne 25072;* Santa Cruz de Parra, *Lindman A2853.* PARÁ: 2 km. S Baião, *Drouet 1992.* RIO DE JANEIRO: Isla Paqueta, *Dusén 5.*

BOLIVIA. SANTA CRUZ: Portachuelo, *Steinbach 3235;* W of Río Parai, *Herzog 1362;* Río Ibon, *O. E. White 2088,* type of *F. fragile* Rusby.

PARAGUAY: Asunción, *Morong 681, Malme s. n.;* Carapeguá, *Rojas 3220; Ypacaray, Hassler 72118;* Pilcomayo River, *Morong 1526;* Laguna Ypacaray, *Fiebrig 331, Hassler 12118;* Santa Elisa, *Hassler 2760;* between Río Apa and Río Aquidaban, *Fiebrig 4250.*

ARGENTINA. CHACO: Fontana, *T. Meyer 215;* La Fidelidad, *Jörgensen 3037.* FORMOSA: Formosa, *Jörgensen 1918, 2606;* Gubernación Formosa, *Kermes 380.* JUJUY: San Pedro de Jujuy, *Schreiter 5207.* SALTA: Orán, *Schreiter 33559, 10842;* Embaración, *Schreiter 5227.* SANTA FE: Los Amores, Generál Obligado, *Ragonese 3235.*

Series 3. CYNANCHOIDES R. Holm, ser. nov.

Inflorescentia ut videtur lateralis umbelliformis, cyma una, pedunculo quam internodio subjacenti angustiore (interdum obsoleto).

Type species: *Sarcostemma cynanchoides* Decne.

This largest series of the subgenus CERAMANTHUS includes those species which have lateral inflorescences borne upon peduncles not equalling the subjacent internode in thickness. They represent an apparently natural group which, however, is further divisible into groups of closely related species. These subdivisions have not been recognized nomenclaturally, but their relationships are discussed in connection with the particular species which they include, and are also expressed in the key.

KEY TO THE SPECIES

a. Leaves very broadly ovate-cordate to orbicular, the base cordate with converging lobes.
  b. Petals strongly reflexed at maturity; ring of the corona relatively long and conspicuous; column nearly equalling the corona vesicles in length; corona vesicles ovoid to pyramidal. Plants of Mexico, Central America, and northeastern South America ..... 4. *S. bilobum*
  bb. Petals not reflexed at maturity; ring of the corona relatively short; column nearly obsolete; corona vesicles ovoid; leaves long-mucronate, conspicuously paler beneath. Plants of Guatemala ..... 5. *S. odoratum*
aa. Leaves broadly to narrowly lanceolate, the base usually cordate with descending or diverging lobes, obtuse or cuneate in very narrow leaves.
  b. Petals strongly reflexed at maturity; leaves long, linear. Plants of South America ..... 6. *S. gracile*
  bb. Petals not strongly reflexed at maturity; leaves lanceolate to linear. Plants of North America.
    c. Column exceeding the corona vesicles in length; vesicles of the corona constricted at their insertion upon the column; leaves very long, narrowly lanceolate, the margin usually undulate-crispate; follicles very attenuate ..... 7. *S. crispum*
    cc. Column shorter than the corona vesicles; vesicles of the corona not constricted at their insertion upon the column; leaves lanceolate to linear, the margin not undulate-crispate.
      d. Corolla segments more than 6.5 mm. long, sepals more than 3.5 mm. long; leaves broadly lanceolate, the base cordate with descending lobes (rarely diverging or converging); relatively stout vines with few lateral branches. Plants of Texas and Mexico.
        e. Column relatively long; stigma-head apiculate; leaves about twice as long as broad; peduncle usually shorter than the subtending leaves or obsolete. Plants of central Mexico ..... 8. *S. elegans*
        ee. Column relatively short; stigma-head obscurely bilobed; leaves about three or more times as long as broad; peduncle usually exceeding the subtending leaves. Plants of Texas and northern Mexico ..... 9. *S. Torreyi*
      dd. Corolla lobes less than 6.5 mm. long, sepals less than 3 mm. long; leaves lanceolate to linear, the base cordate with diverging (rarely descending or converging) lobes, or obtuse to cuneate.
        e. Leaves broadly lanceolate to linear, the base cordate or hastate (rarely obtuse); ring of the corona free from the corona vesicles ..... 10. *S. cynanchoides*
        ee. Leaves narrowly lanceolate to linear or oblanceolate, the base obtuse to cuneate; ring of the corona adnate to the base of the corona vesicles.

f. Leaves narrowly lanceolate to linear; stems and leaves densely canescent; corolla lobes 4–5 mm. long. Plants of the southwestern United States..... 11. *S. hirtellum*

ff. Leaves oblanceolate; stems and leaves puberulent; corolla lobes 4.5–6.0 mm. long. Plants of Baja California..... 12. *S. arenarium*

4. SARCOSTEMMA BILOBUM Hook. & Arn. Bot. Beech. Voy. 438. 1841.

KEY TO THE SUBSPECIES

a. Leaves broadly ovate-cordate to orbicular, acuminate to submucronate; pollinium-sacs oblongoid-cylindrical, about four times as long as broad, the corpusculum narrowly sagittate; vesicles of the corona widest above the middle..... 4a. *S. bilobum* ssp. *bilobum*

aa. Leaves oblong-orbicular, mucronate; pollinium-sacs quadrate-oblongoid, somewhat flattened, two or three times as long as broad, the corpusculum broadly sagittate; vesicles of the corona widest below the middle..... 4b. *S. bilobum* ssp. *Lindenianum*

4a. SARCOSTEMMA BILOBUM Hook. & Arn. ssp. **bilobum** (Hook. & Arn.) R. Holm, stat. nov.

Sarcostemma bilobum Hook. & Arn. Bot. Beech. Voy. 438. 1841. (T.: *Beechey Herb. s. n. in Herb. Kew.*!).
Philibertia biloba (Hook. & Arn.) Gray, in Proc. Amer. Acad. 21:395. 1886.
Philibertia refracta Donn. Sm. in Bot. Gaz. 18:207. 1893. (T.: *Gomez 787 in U. S. Nat. Herb.*!).
Funastrum refractum (Donn. Sm.) Schltr. in Fedde's Repert. 13:287. 1915.
Funastrum bilobum (Hook. & Arn.) Macbr. in Contr. Gray Herb. n. s. 49:51. 1917.
Sarcostemma bellum Standl. & L. Wms. in Ceiba 1:90. 1950, ex char.

Stems twining or trailing, green, glabrescent to puberulous-pilose; lateral branches normally few. Leaves broadly ovate-cordate to orbicular, acuminate to submucronate, deeply cordate, the lobes usually converging, 3–5 cm. long, 2–5 cm. wide, membranaceous to subcoriaceous, glabrescent to puberulent on both surfaces, with one or more glands on the midrib at the base; petiole 1.5–3.0 cm. long. Inflorescences umbelliform, 9- to 44-flowered; peduncle 4–5 cm. long, glabrescent to puberulent; bracts usually linear, 1–2 mm. long, occasionally foliaceous and lanceolate; pedicels slender, 1.5–3.0 cm. long, more or less puberulent. Calyx lobes narrowly lanceolate, 2–3 mm. long, puberulent on both surfaces; squamellae absent or solitary. Corolla rotate-subcampanulate, yellowish-white, the tube 1.5 mm. long, the lobes reflexed at maturity, narrowly ovate, obtuse, revolute, 5–6 mm. long, glabrous to puberulous-papillate without, minutely pilosulose within, obscurely ciliolate. Gynostegium 3.0–3.5 mm. high, the column 1.5 mm. long. Anthers 1.5 mm. long, the apical appendage orbicular, emarginate, the pollinium-sacs oblongoid-cylindrical, 1 mm. long, with narrowly sagittate corpusculum; ring of the corona prominent, 1 mm. long, not adnate to the base of the corona vesicles; vesicles of the corona pyramidal, widest above the middle, 1.5–2.0 mm. long. Ovaries 1.5–2.0 mm. long, glabrous, the styles very sparsely pilosulose; stigma-head obscurely 2-apiculate. Follicles narrowly fusiform, attenuate, 8 cm. long, 1.5 cm. thick, minutely puberulent; seeds unequally biconvex, 5 mm. long, 3 mm. wide, rugose-papillate dorsally, papillate ventrally; coma about 3 cm. long.

The systematics of the Central America Sarcostemmas with reflexed corolla lobes long has been confused. A number of species have been described on the

basis of slight differences, chiefly in pubescence, and the names *S. odoratum* and *S. elegans* have been misapplied to these plants. Considering the problem as a whole I have been unable to distinguish more than one species, which is quite distinct from the true *S. odoratum*. At least two infraspecific entities are present, however, and their intergradation and enigmatic distribution still leave the taxonomy in an unsettled state. I have recognized two subspecies separated by the characters given in the key, together with other less tangible differences. *Sarcostemma b. bilobum* occurs, chiefly to the north and west, in Central America and southern Mexico. The putative hybrids have been designated as such since they do not appear to be part of a cline. Ecological data are sadly lacking; if available, they might explain the peculiar distribution of the subspecies. *Sarcostemma b. bilobum* apparently grows in open woods from 3000 to 9000 feet, and flowers from October to December.

Mexico. Chiapas: between Teneapa and Yajalon, *E. W. Nelson 3265;* near Yajalon, *E. W. Nelson 3412.* Colima: Paso del Río, *Emrick 178.* Jalisco: Santa Cruz de Vallarta, *Mexia 1271.* Mexico: Temascáltepec, *Hinton 8473.* Michoacán: Coalcomán, Coahuayana, *Hinton 16249.* Morelos: near Cuernavaca, *Pringle 11887.* Oaxaca: Capital Concordia, *Reko 3513;* near Tehuantepec?, *Seler & Seler 1790.* Yucatán: Izamál, *Gaumer 880* (in part).

Guatemala. Petén: Uaxactun, *Bartlett 12470.* Sacatepequez: Santiago, *Gomez 787,* type of *P. refracta* Donn. Sm.

Honduras. Morazan: Río El Quebracho above Jicarito, *Standley 14814,* type of *S. bellum* Standl. & L. Wms.

British Honduras: Honey Camp, *Lundell LP33, 609.*

Putative Hybrids: listed following *S. bilobum Lindenianum* (4b).

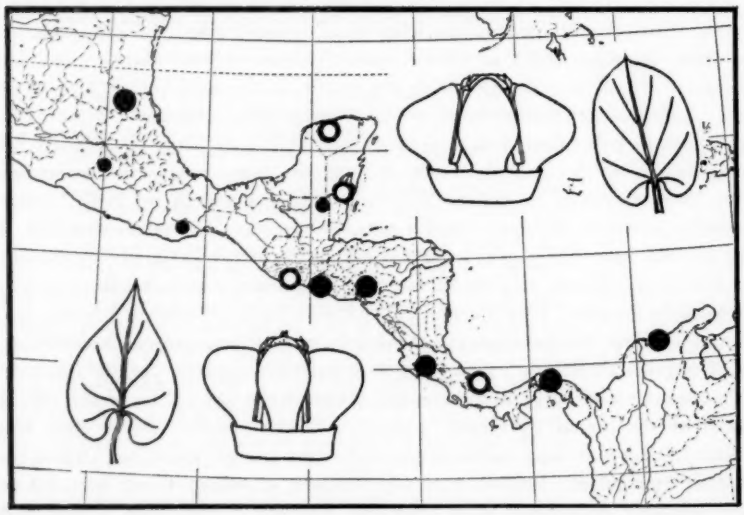

Fig. 8. Gynostegium and leaf of *S. bilobum bilobum* (lower left), of *S. bilobum Lindenianum* (upper right); distribution of *S. bilobum bilobum* (small dots), of *S. bilobum Lindenianum* (large dots), of putative hybrids, black circles.

4b. SARCOSTEMMA BILOBUM Hook. & Arn. ssp. **Lindenianum** (Decne.) R. Holm, stat. nov.

Sarcostemma Lindenianum Decne. in DC. Prodr. 8:541. 1844. (T.: *Linden s. n. in Herb. Paris*!).
Philibertia Lindeniana (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.
Philibertia Ervendbergii A. Gray, in Proc. Amer. Acad. 21:395. 1886. (T.: *Ervendberg 174 in Herb. Gray*!).
Philibertia Fendleri A. Gray, loc. cit. 1886. (T.: *Fendler 2119 in Herb. Gray*!).
Philibertia reflexa Pittier, in Contr. U. S. Nat. Herb. 13:96. 1910. (T.: *Pittier s. n. in U. S. Nat. Herb.*!).
Philibertia dumetorum T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:380. 1913. (T.: *Purpus 6013 in Herb. Univ. Calif.*!).
Funastrum Ervendbergii (Gray) Schltr. in Fedde's Repert. 13:285. 1915.
Funastrum Fendleri (Gray) Schltr. loc. cit. 1915.
Funastrum Lindenianum (Decne.) Schltr. loc. cit. 286. 1915.
Funastrum reflexum (Pittier) Schltr. loc. cit. 287. 1915.
Philibertella filipes Rusby, Descr. S. Am. Pl. 94. 1920. (T.: *H. H. Smith 1669 in Herb. N. Y. Bot. Gard.*!).
Funastrum dumetorum (Brandeg.) Standl. in Contr. U. S. Nat. Herb. 23:1172. 1924.

Stems trailing or twining, gray-green, pilosulose; lateral branches normally few. Leaves oblong-orbicular, mucronate, deeply cordate, the lobes usually converging, 2–5 cm. long, 1.5–4.0 cm. wide, subcoriaceous, densely pilosulose on both surfaces, rarely glabrous, with one or more glands on the midrib at the base; petiole 1.0–2.5 cm. long. Inflorescences umbelliform, 7- to 10-flowered; peduncle 1.5–2.0 cm. long, subpilose; bracts usually linear, minute, occasionally foliaceous and ovate; pedicels 1–2 cm. long, subpilosulose. Calyx lobes linear to ovate, 2.5 mm. long, pilosulose without, glabrate within; squamellae usually solitary. Corolla rotate-subcampanulate, whitish with a median purple streak on each lobe, the tube 2 mm. long, the lobes reflexed at maturity, lanceolate, obtuse, 5.5 mm. long, glabrescent without, appressed-pilosulose within, ciliolate. Gynostegium 4 mm. high the column 1.5 mm. long. Anthers 1.5 mm. long, the apical appendage reniform, emarginate, the pollinium-sacs quadrate-oblongoid, somewhat flattened, 0.8 mm. long, with broadly sagittate corpusculum; ring of the corona thick, revolute, not adnate to the base of the corona vesicles; vesicles of the corona pyramidal, widest below the middle, 2 mm. long. Ovaries 2 mm. long, glabrous; stigma-head abruptly 2-apiculate to umbonate. Follicles obclavate, attenuate, 7 cm. long, 2 cm. thick, puberulent, finely striate; seeds somewhat flattened, 7 mm. long, 4 mm. wide, minutely papillate on both surfaces; coma about 3 cm. long.

The relationship of this subspecies with S. *b. bilobum* has been described in the discussion of the latter. *Sarcostemma b. Lindenianum* occurs, roughly to the south and east, in Mexico and Central America and extends into Colombia and Venezuela. The few data available indicate that it is found at much lower altitudes, from 50 to 80 feet above sea level, and blooms from July to September. Thus the isolating mechanisms may be in part ecological. I believe that mechanical difficulties attendant with hybridization also play an important part, in view of the differences in the pollinia.

MEXICO. CHIAPAS: Tonalá, *Purpus 6651*. SAN LUIS POTOSÍ: Rascón, *Purpus 5494, 5256*. VERA CRUZ: Acasonica, *Purpus 8412;* Baños del Corizál, *Purpus 6013*, type of *P. dumetorum* Brandeg.; Wartenburg, near Tantoyuca, *Ervendberg 174*, type of *P. Ervendbergii* Gray. YUCATÁN: Izamál, *Gaumer 880* (in part).

HONDURAS. VALLE: San Lorenzo, *Rodriguez 3486, 3331*.

EL SALVADOR: Acajutla, *Calderón 1676*.

COSTA RICA: near San Mateo, *Biolley 7095;* Nicoya, *Pittier s. n.*, type of *P. reflexa* Pittier; vic. Cascajál, 25 km. ESE of Puntarenas, *Holm & Iltis 272*.

PANAMA. PANAMA: banks of Mamoni River, above Chepo, *Pittier 4728*.

COLOMBIA. MAGDALENA: Santa Marta, *H. H. Smith 1669*, type of *P. filipes* Rusby.

VENEZUELA. MÉRIDA: Tovar, *Fendler 2119*, type of *P. Fendleri* Gray.

PUTATIVE HYBRIDS. MEXICO. YUCATÁN: Izamál, *Gaumer 880* (in part). PANAMA. BOCAS DEL TORO: near Chiriquí Lagoon, *Wedel 1755*. GUATEMALA. ESCUINTLA: Santa Lucía, *Heyde & Lux 47, 6353*. BRITISH HONDURAS: Corozál District, Santa Rita, *Gentle 829;* San Andrés, *Gentle 553*.

5. SARCOSTEMMA **odoratum** (Hemsl.) R. Holm, comb. nov.

Philibertia odorata Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:319. 1881. (T.: *Salvin s. n. in Herb. Kew.*!).
Funastrum odoratum (Hemsl.) Schltr. in Fedde's Repert. 13:286. 1915.

Stems twining, gray-green, pilosulose to pilose; lateral branches normally few. Leaves narrowly to broadly ovate, long-mucronate, deeply cordate, the lobes converging, 3.5–5.0 cm. long, 2.0–4.5 cm. wide, subcoriaceous, pilosulose above, densely puberulous-pilose beneath, with one or more glands on the midrib at the base; petiole 2.5–4.0 cm. long. Inflorescences umbelliform, 6- to 12-flowered; peduncle 1.5–3.0 cm. long, pilosulose; bracts linear, minute; pedicels 1.5–2.0 cm. long, pilosulose. Calyx lobes narrowly lanceolate, 4 mm. long, subpilose without, glabrous within; squamellae usually solitary. Corolla rotate-subcampanulate, white, the tube 1 mm. long, the lobes ovate, 5 mm. long, pilosulose without, puberulous-papillate within. Gynostegium 2.5 mm. high, the column nearly obsolete. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs cylindrical, 0.75 mm. long, with sagittate corpusculum; ring of the corona thick, revolute, scarcely adnate to the base of the corona segments; vesicles of the corona ovoid, 2 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head abruptly 2-apiculate. Follicles and seeds unknown.

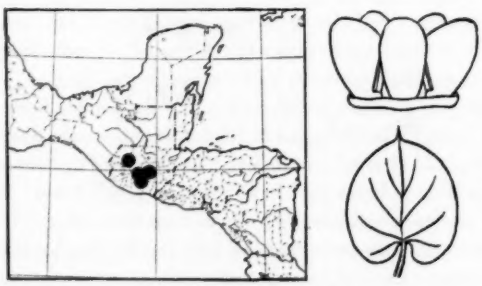

Fig. 9. Distribution, gynostegium and leaf of *S. odoratum*.

Sarcostemma odoratum is a rare species known only from Guatemala. The converging basal lobes of the leaves and characters of the gynostegium ally it with *S. bilobum;* it lacks the long column and reflexed corolla lobes of that species, however. It has been collected on hillsides from 4000 to 5000 feet; apparently it flowers from August to September.

GUATEMALA. CHIMALTENANGO: Chimaltenango, *J. R. Johnston 752.* GUATEMALA: *Aguilar 313.* HUEHUETENANGO: between San Sebastian H. and large peñasco above town, *Steyermark 50514.* SACATEPEQUEZ: Volcán de Fuego, *Salvin s. n.*, type of *P. odorata* Hemsl. DATA INCOMPLETE: Brenas, *Tonduz 785.*

6. SARCOSTEMMA GRACILE Decne. in DC. Prodr. 8:539. 1844. (T.: *Tweedie 1837 in Herb. Kew.*!).

Amphistelma exsertum Griseb. Symb. Fl. Arg. 229. 1879, ex char. (T.: *Lorentz & Hieronymous 1125*).
Sarcostemma carpophylloides Morong, Enum. Pl. Paraguay (Ann. N. Y. Acad. Sci. 7:) 165. 1893. (T.: *Morong 1004 in Herb. N. Y. Bot. Gard.*!).
Philibertia exserta (Griseb.) Schltr. in O. Ktze. Rev. Gen. 3:200. 1898.
Ceramanthus gracilis (Decne.) Malme, in Ark. Bot. 4^{14}:2. 1905.
Funastrum gracile (Decne.) Schltr. in Fedde's Repert. 13:285. 1915.

Stems twining, green, glabrous, the nodes puberulent; lateral branches many. Leaves narrowly lanceolate or linear, acute to acuminate, obtuse to cuneate, involute proximally 1–2 mm., 3.0–5.5 mm. long, 0.2–0.5 cm. wide, membranaceous, glabrate to minutely puberulent above and beneath, with no glands on the midrib at the base; petiole 0.1 cm. long. Inflorescences umbelliform, 8- to 16-flowered; peduncle 3.5–7.0 cm. long, glabrate to very minutely puberulent; bracts linear, minute; pedicels 0.9–1.5 cm. long, pilosulose. Calyx lobes lanceolate, 1.5 mm. long, minutely pubescent without, glabrous within; squamellae absent. Corolla rotate-subcampanulate, white, the tube 1 mm. long, the lobes reflexed, ovate, acute, 3.5 mm. long, glabrate without, minutely papillate within ciliolate. Gynostegium 2 mm. high, the column 1.5 mm. long. Anthers 1 mm. long, the apical appendage reniform, the pollinium-sacs oblongoid-cylindrical, 0.75 mm. long with sagittate corpusculum; ring of the corona thick, adnate to the base of the corona vesicles, vesicles of the corona ovoid, pointed at the tip, 1.5 mm. long. Ovaries 1.5 mm. long, essentially glabrous; stigma-head conical, obscurely 2-lobed. Follicles narrowly fusiform, 3.5–5.5 cm. long, 0.4–0.5 cm. thick, minutely puberulent; seeds somewhat flattened, 4 mm. long, 1.5 mm. wide, the margin flat and obscurely serrate; coma about 1 cm. long.

The small flowers with reflexed corolla lobes and the linear leaves separate this species at once from all other South American forms. Since it is distant from any species remotely resembling it, I hesitate to speculate as to its affinities. There is something reminiscent of *S. glaucum* in the floral structure and inflorescence, but the species hardly can be referred to series CLAUSA since the peduncle does not equal the stem in thickness and only rarely bears two cymes. This species may represent an extreme modification of the ancestral form of series CLAUSA.

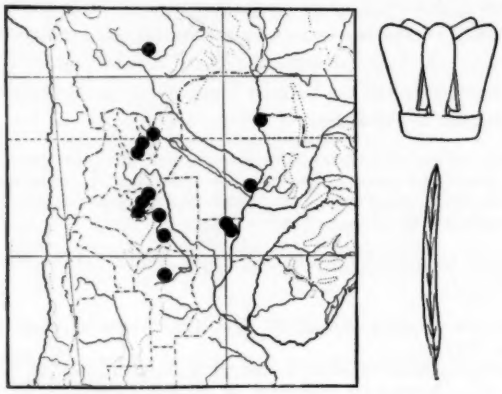

Fig. 10. Distribution, gynostegium, and leaf of *S. gracile*.

Sarcostemma gracile inhabits the *llanos* of northern Argentina and adjacent Bolivia and Paraguay. According to Meyer, it is halophytic, a fact which may account for its obvious reduction. It flowers from October to March.

BOLIVIA. SANTA CRUZ: Chilón, *Steinbach 3964*. CHACO: Curupenda, *Cárdenas 2521*; Tatarenda, *Fries 1441*.

PARAGUAY: Chaco Paraguayo, Puerto Casado, *Rojas 2482*; Santa Elisa, *Rojas 2715*; Pilcomayo River, *Morong 1004*, type of *S. carpophylloides* Morong.

ARGENTINA. CATAMARCA: Capitál, *Castillón 1065*. CHACO: Fontana, *T. Meyer 219*. CÓRDOBA: Córdoba, *Kurtz 4510*, *Lassen 86*; Sierra Chica, *Kurtz 207*. FORMOSA: Formosa, *Jörgensen 2599*; Las Lomitas, *Parodi 8436*. JUJUY: San Pedro, *Venturi 5318*; Perico del Carmen, Estancia Peruco, *Venturi s. n.* LA RIOJA: Famatina, *Venturi 7828*; La Antigua, Pozo de la Orilla, *Castellanos s. n.* SALTA: Orán, Tartagal Villa, *Schreiter 10844*, *3573*; 5 km. NW Embarcación, *West 8443*. SANTA FE: Generál Obligado, Los Amores, *Ragonese 3115*. SANTIAGO DEL ESTERO: La Banda, *Lillo 6091*; Recreo, *Stuckert 23009*; between Brea Pozo & Río Huayco Hondo, *Bartlett 19753*. TUCUMÁN: Burruyacu, El Timbo, *Venturi 1718*; Río Lules, *Lillo 7860*; Cruz Alta, Orillas Río Sali, *Venturi 753*; Campo Alegre, *Schreiter 5915*; Famailla, Bella Vista, *Venturi 2730*.

7. SARCOSTEMMA CRISPUM Benth. Pl. Hartw. 291. 1848. (T.: *Hartweg s. n.*!).

Sarcostemma heterophyllum Engelm. ex Torr. Pac. R. R. Rept. 5(App.):362. 1857. (T.: *Wright 1679*!).
Sarcostemma undulatum Torr. in Bot. Mex. Bound. Surv. 161. 1859. (T.: *Parry s. n.*!).
Philibertia undulata (Torr.) Gray, in Proc. Amer. Acad. 12:65. 1877.
Philibertia linearis (Decne.) A. Gray, var. *heterophylla* (Engelm. ex Torr.) Gray, Syn. Fl. 2^1:88. 1878, as to basinym only.
Philibertia crispa (Benth.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.
Philibertella crispa (Benth.) Vail, in Bull. Torr. Bot. Club 24:307. 1897.
Philibertella Hartwegii heterophylla (Engelm. ex Torr.) Vail, loc. cit. 1897, as to basinym only.
Philibertella heterophylla (Engelm. ex Torr.) Cocker. in Bot. Gaz. 26:279. 1898, as to basinym only.
Funastrum crispum (Benth.) Schltr. in Fedde's Repert. 13:284. 1915.

Funastrum lineare (Decne.) Macbr. var. *heterophyllum* (Engelm. ex Torr.) Macbr. in Contr. Gray Herb. n. s. 49:50. 1917, as to basinym only.
Funastrum heterophyllum (Engelm. ex Torr.) Standl. in Contr. U. S. Nat. Herb. 23:1170. 1924, as to basinym only.
Philibertia heterophylla (Engelm. ex Torr.) Jepson, Man. Fl. Pl. Calif. 770. 1925, as to basinym only.
Sarcostemma lobata Waterfall, in Rhodora 51:58. 1949. (T.: *Waterfall 7914 in Herb. Univ. Okla.*!).

Stems twining or trailing, green, glabrate to puberulent, the nodes densely white-pubescent; lateral branches few. Leaves narrowly to broadly lanceolate, acuminate, hastate, cordate or truncate, usually strikingly undulate-crispate, rarely not crispate, 3–10 cm. long, 0.5–3.0 cm. wide, subcoriaceous, puberulent above, the midrib usually white-pilose, without glands at the base, puberulent beneath, the midrib usually white-glabrous; petiole 0.4–0.8 cm. long. Inflorescences umbelliform, 4- to 7-flowered; peduncle 0.3–3.0 cm. long, glabrescent, much shorter than the subtending leaves; bracts linear, minute; pedicels 1.5–2.0 cm. long, glabrescent. Calyx lobes narrowly lanceolate, 3–6 mm. long, copiously puberulent on both surfaces; squamellae solitary, rarely paired. Corolla rotate-subcampanulate, greenish purple without, purple within, the tube 1 mm. long, the lobes ovate-elliptic, obtuse, 7–11 mm. long, puberulent without, glabrous within, ciliate. Gynostegium 3 mm. high, the column 1 mm. long. Anthers 1 mm. long, the apical appendage ovate, the pollinium-sacs oblongoid-cylindrical, 0.8 mm. long, with sagittate corpusculum; ring of the corona thin, revolute, scarcely adnate to the column; vesicles of the corona thin, revolute, scarcely adnate to the column; vesicles of the corona oblongoid-ovoid, constricted at their insertion upon the column, 1 mm. long. Ovaries 2 mm. long, glabrescent; stigma-head abruptly and shortly 2-apiculate. Follicles narrowly fusiform, long-attenuate, 8.5–12.3 cm. long, 1.3–1.9 cm. thick, puberulent, finely striate; seeds unequally biconvex, 7 mm. long, 3 mm. wide, obscurely rugose dorsally, minutely papillate ventrally; coma about 3 cm. long.

The crispate leaves and large, deep purple flowers combine to make this one of the most distinctive species in the genus. There is a poorly defined cline in the characters of the leaves: to the south and west the leaves generally are smaller, less crisped, and less pubescent on the midrib. I have seen specimens from Mexico which show no signs of crisping and have very narrowly lanceolate leaves. The ends of the cline are not sufficiently distinct for taxonomic recognition, however. I cannot conceive that this cline is the result of anything but a response to increasing aridity which leads to reduction of the lamina and consequent suppresion of the marginal growth responsible for crispature. Since floral differences do not exist, hybridization probably does not play a role.

The rather confused synonymy of this species is explained in the discussion pertaining to *Sarcostemma cynanchoides* ssp. *Hartwegii*. *Sarcostemma crispum* seems nowhere to be common; Reverchon reports it to be local and rare around Dallas, Midland, and Austin, Texas, and other collectors indicate that it usually

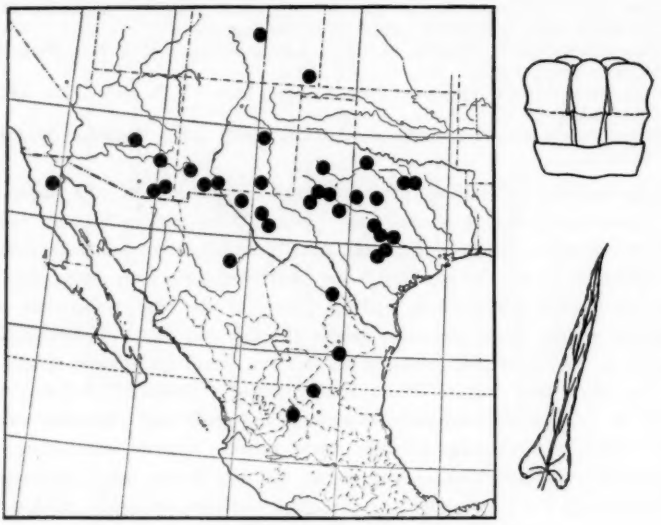

Fig. 11. Distribution, gynostegium, and leaf of S. *crispum*.

occurs scatteringly or in very small colonies. It grows at altitudes of 4000 to 7000 feet, chiefly in open, dry, rocky, or stony ground, and has been found in chaparral associated with *Zizyphus* and *Fallugia*. The blooming season ranges from May 9 to August 24. Fruiting specimens have been collected from May 13 to August 24. The distribution is from Colorado through Texas, New Mexico, and Arizona to central Mexico.

UNITED STATES. COLORADO: BACA CO.: S of Pritchett, *Harrington 3353;* FREMONT CO.: Phantom Canyon, *Christ 1090.* OKLAHOMA: CIMARRON CO.: N of Black Mesa, 3 mi. N of Kenton, *Waterfall 7914,* type of S. *lobata* Waterfall. TEXAS: BAYLOR CO.: Seymour, *Reverchon s. n.;* BEXAR CO.: San Antonio, *Schulz 793;* BLANCO CO.: *Wright 1678;* BREWSTER CO.: *Ferris & Duncan 2631;* CALLAHAN CO.: Baird, *E. J. Palmer 13688;* COMAL CO.: Fischer's Store, *E. J. Palmer 12209;* DALLAS CO.: Dallas, *Reverchon 601;* EASTLAND CO.: Eastland, *Oyster 2595;* GILLESPIE CO.: Grape Creek, *Jermy 134;* HOWARD CO.: Big Spring, *Eggert s. n.;* HUDSPETH CO.: Eagle Mts. near Hot Wells, *Waterfall 4964;* JEFF DAVIS CO.: Limpia, *Young 27;* LLANO CO.: *Bray 336½;* LUBBOCK CO.: Lubbock, *Reed 3694;* MIDLAND CO.: Midland, *Tracy 7980;* MITCHELL CO.: Colorado, *Eggert s. n.;* TARRANT CO.: *Ruth 740;* TAYLOR CO.: Abilene, *Tracy 7979;* TOM GREEN CO.: Dove Creek, *Tweedy 235;* TRAVIS CO.: Austin, *E. Hall 518.* NEW MEXICO: DONA ANA CO.: Organ Mts., *Wooton s. n.;* EDDY CO.: Queen, *Wooton s. n.;* GRANT CO.: Central, *Mulford 406;* GUADALUPE CO.: Santa Rosa, *Arsène 19470;* LUNA CO.: Deming, *Goldman 1445.* ARIZONA: COCHISE CO.: Rhoda Rigg's Ranch, Chiricahua Mts., *Blumer 1499;* GILA CO.: Collom Camp, Matzatzal Mts., *Collom 575;* GRAHAM CO.: 10 mi. above Clifton, *Hough s. n.*

MEXICO. BAJA CALIFORNIA NORTE: near Ciénaga, S end of Sierra Juárez, *Wiggins 9148.* CHIHUAHUA: near Chihuahua, *Pringle s. n., 546, 1326;* W from Pearson, *Barlow s. n.;* Sta. Eulalia Plains, *Wilkinson s. n.* COAHUILA: 5 km. NE Sta. Elena, *R. M. Stewart 605;* 2–3 km. N Puerto Colorado, *I. M. Johnston 8681;* San Lázaro, *Wynd & Muller 101.* NUEVO LEON: 15 miles SW Galeana, *Muller & Muller 1084.* SAN LUIS POTOSÍ: Charcas, *Lundell 5074.*

8. SARCOSTEMMA ELEGANS Decne. in DC. Prodr. 8:541. 1844. (T.: *Berlandier 602 in Herb. Paris*!).

Sarcostemma bicolor Decne. loc. cit. 1844. (T.: *Galeotti 1537 in Herb. Paris*!).
Sarcostemma luridum Kunze, in Linnaea 20:26. 1847, ex char. (T.: *Schleiden s. n.*).
Philibertia elegans (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.
Philibertia lurida (Kze.) Hemsl. loc. cit. 319. 1881.
Philibertia bicolor (Decne.) Gray, in Proc. Amer. Acad. 21:395. 1886.
Philibertella elegans (Decne.) Vail, in Bull. Torr. Bot. Club 24:310. 1897.
Funastrum elegans (Decne.) Schltr. in Fedde's Repert. 13:284. 1915.
Funastrum luridum (Kze.) Schltr. loc. cit. 286. 1915.
Funastrum bicolor (Decne.) Macbr. in Contr. Gray Herb. n. s. 49:50. 1917.
Funastrum bicolor (Decne.) Standl. in Contr. U. S. Nat. Herb. 23:1172. 1924.

Stems twining or trailing, gray-green, glabrescent to copiously pilosulose; lateral branches few. Leaves broadly lanceolate to oblong, acute to mucronate, deeply cordate, the lobes descending, 2–5 cm. long, 1.0–4.5 cm. wide, subcoriaceous, glabrescent to copiously puberulent on both surfaces, with one or more glands on the midrib at the base; petiole 0.6–2.2 cm. long. Inflorescences umbelliform, 4- to 7-flowered; peduncle 0.5–1.8 cm. long, minutely puberulent, much shorter than the subtending leaves; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–2.5 cm. long, puberulent. Calyx lobes ovate, 4–6 mm. long, densely puberulent without, puberulent within; squamellae alternate, usually solitary. Corolla rotate-subcampanulate, yellow, with a deep purple spot at the base of each lobe, often extending upward as a median streak, or entirely suffused with purple on the inner surface, greenish without, the tube 3.5 mm. long, the lobes ovate-lanceolate, obtuse, 9–13 mm. long, minutely puberulent without, glabrescent within. Gynostegium 3.5 mm. high, the column about 1 mm. long. Anthers 1.5 mm. long, the apical appendage suborbicular, the pollinium-sacs oblongoid-cylindrical, 0.7 mm. long, with sagittate corpusculum; ring of the corona thin, adnate to the base of the corona vesicles; vesicles of the corona oblongoid to subspheroid, the inner side often apiculate at the tip, or with a vertical keel, 2.5 mm. long. Ovaries 2.5 mm. long, glabrous; stigma-head conical, with 2 long apiculae. Follicles narrowly fusiform-obclavate, 7.6 cm. long, 1.2 cm. thick, minutely puberulent, finely striate; seeds unequally biconvex, 7 mm. long, 3 mm. wide, obscurely rugose on both surfaces; coma about 3 cm. long.

Sarcostemma elegans is closest, morphologically, to S. *Torreyi*, from which it differs in the short peduncles, relatively short leaves, and the long, apiculate stigma-head. S. *elegans* occurs in the Central Plateau region of Mexico, while S. *Torreyi* is found in the northern desert areas of Mexico and adjacent Texas. As indicated in the key, the two species form a close-knit group more or less isolated from the other species in the section. Probably they have either differentiated from a common ancestor occupying the area from central Mexico to Texas, or the southern species may have migrated to the north giving rise to S. *Torreyi* in this changed habitat. The floral differences between the species are such that hybridization would appear to be difficult, e. g. the length of the column and stigma-head

appendages in S. *elegans* would result in the pollinia being affixed to different insects or to different places upon the same species of insect. There is a narrow gap in the ranges; however, there are several specimens *(Stanford, Retherford & Northcraft 869, Reko 5259)* which I interpret as hybrids between S. *elegans* and S. *Torreyi*. Apparently these are back-crosses, for they are sufficiently close to one or the other of the putative parents to be easily referred to either species. The precise effects of this hybridization cannot be determined without the use of population studies. The most satisfactory way of handling such a problem taxonomically appears to be to refer the hybrids to whichever species they are morphologically and geographically closest. Unfortunately, this has the disadvantage of obscuring the interesting genetic implications. *Funastrum vesiculare* apparently is a hybrid which is very close to S. *Torreyi*, from which it differs, however, in the direction of S. *elegans;* I have referred it to the former species.

Sarcostemma elegans has been found growing chiefly on rocky slopes or lava fields at altitudes from 5000 to 8000 feet. Flowering specimens are dated from January 1 to October 27; the single fruiting specimen is dated August 2.

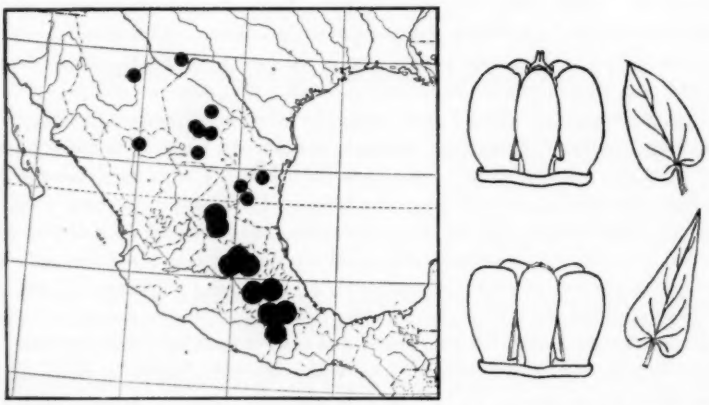

Fig. 12. Gynostegium and leaf of S. *elegans* (upper row), of S. *Torreyi* (lower row). Distribution of S. *elegans* (large dots), of S. *Torreyi* (small dots).

MEXICO. DISTRITO FEDERÁL: Pedregál, *Lyonnet 29;* San Gerónimo, *Russell & Souviron 127;* near Mexico City, *Berlandier 602,* type of S. *elegans* Decne. GUANAJUATO: Guanajuato, *Duges 101.* HIDALGO: Ixmilquilpan, *Purpus 1379; Rose, Painter & Rose 8943.* JALISCO: near Zapotlán, *Pringle 5496.* MÉXICO: Temascáltepec, Socobon, *Hinton 7225;* Crucero Agua Blanca, *Hinton 4936;* Valley of México, near San Angel, *Rose, Painter & Rose 9499;* near Tlalpam, *Rose, Painter & Rose 8250, Pringle 13116, Rose & Hough 4529;* Santa Fe, *Bourgeau 318.* MICHOACÁN: Coalcomán, Barroloso, *Hinton 15075.* OAXACA: Nochixtlan, barrancas de Puebla Viejo, *Conzatti 1842;* Tenango, *L. C. Smith 390.* PUEBLA: near San Luis Tultitlanapa, *Purpus 3241;* near Tehuacán, *Pringle 6760, Mohr s. n., Rose, Painter & Rose 9953, Galeotti 1537,* type of S. *bicolor* Decne.; El Riego, *Purpus 1258;* Rancho Posado, *Nicolas 47.* QUERETARO: near San Juan del Río, *Rose, Painter & Rose*

9669, Altamirano 1973. SAN LUIS POTOSÍ: Bocas, *Pringle 3564;* Silos, *Purpus 482;* near San Luis Potosí, *Parry & Palmer 589, Schaffner 316;* mts. near San Miquelito, *Schaffner 649.* TLAXCALA: Tlaxcala, *Balls 4908.* VERA CRUZ: Orizaba, *Botteri 979.*

9. SARCOSTEMMA TORREYI (Gray) Woods. in Ann. Mo. Bot. Gard. 28:217. 1941.

Philibertia Torreyi A. Gray, in Proc. Amer. Acad. 12:64. 1877. (T.: *Parry s. n.*!).
Philibertella Torreyi (Gray) Vail, in Bull. Torr. Bot. Club 24:309. 1897.
Funastrum Torreyi (Gray) Schltr. in Fedde's Repert. 13:287. 1915.
Funastrum vesiculare Woods. in Amer. Jour. Bot. 22:687. 1935. (T.: *Bartlett 10318 in Herb. Univ. Mich.*!).

Stems twining or trailing, gray or green, pilosulose; lateral branches few. Leaves lanceolate, acuminate to acute, cordate, the lobes descending, 1.5–4.0 cm. long, 1.0–2.5 cm. wide, subcoriaceous, pilosulose on both surfaces with one or more glands on the midrib at the base; petiole 0.7–1.4 cm. long. Inflorescences umbelliform, 7- to 10-flowered; peduncle 1.0–3.5 cm. long, pilosulose; bracts linear, 0.1–0.2 cm. long; pedicels 0.8–1.6 cm. long, pilosulose. Calyx lobes ovate-lanceolate, 4–6 mm. long, puberulent on both surfaces; squamellae solitary, rarely paired. Corolla rotate-subcampanulate, cream-colored with a purple spot at the base and a median purple spot on each lobe, lobes ovate, acute, 7–11 mm. long, minutely puberulent without, glabrate within, scarious-ciliate. Gynostegium 3 mm. high, the column very short. Anthers 1.5 mm. long, the apical appendage suborbicular to subreniform, the pollinium-sacs oblongoid-cylindrical, 0.8 mm. long, with sagittate corpusculum; ring of the corona fleshy, adnate to the base of the corona vesicles; vesicles of the corona oblongoid to obovoid, 2.5 mm. long. Ovaries 2.5 mm. long, glabrous; stigma-head subconical, obscurely bilobed. Follicles fusiform, long-attenuate, 8.2 cm. long, 1.2 cm. thick, finely striate; seeds somewhat flattened, 7 mm. long, 4 mm. wide, minutely papillate on both surfaces; coma about 3 cm. long.

A relatively rare and local species, the relations of which to S. *elegans* are discussed in connection with the latter. *Sarcostemma Torreyi* inhabits dry hillsides and scrubby woodland associations in northern Mexico and southwestern Texas. It has been collected at altitudes of 4500 to 7200 feet. Judging by the relatively few specimens, it flowers from May 29 to August 18; fruits have been collected in July and September.

UNITED STATES. TEXAS: BREWSTER CO.: Chisos Mts., *Sperry 481;* PRESIDIO CO.: Fresno Canyon, N of Lajitas, *Cutler 1893.*

MEXICO. CHIHUAHUA: Sta. Eulalia Mts., *Pringle 63, 550, 1325.* COAHUILA: Muzquiz, slopes of Sierra de San Manuel, *Wynd & Muller 331;* Parras, *Purpus 4679, Stanford, Retherford & Northcraft 164;* Cuatro Ciénagas, Sierra de la Madera, *Muller 3168;* Sierra de la Gloria, SE Monclova, *Marsh 1915;* Sierra de Sta. Rosa, S of Muzquiz, *Marsh 1413.* DURANGO: Inde, *Reko 5259.* NUEVO LEON: Dulces Nombres, *Meyer & Rogers s. n.;* Monterrey, *Muller 248.* TAMAULIPAS: Cerro Tinaja, near San José, *Bartlett 10318,* type of *F. vesiculare* Woods.; 22 km. SE of Miquihuana, *Stanford, Retherford & Northcraft 869.*

10. Sarcostemma cynanchoides Decne. in DC. Prodr. 8:540. 1844.

KEY TO THE SUBSPECIES

a. Leaves broadly lanceolate, 3–4 times as long as broad, cordate (rarely truncate) at the base; flowers white, the corona vesicles widest above the middle ..... 10a. *S. cynanchoides* ssp. *cynanchoides*

aa. Leaves narrowly lanceolate, more than 3–4 times as long as broad, hastate (rarely truncate or obtuse); flowers purple or pink, or the corolla lobes with a median purple streak, the corona vesicles widest below the middle ..... 10b. *S. cynanchoides* ssp. *Hartwegii*

10a. Sarcostemma cynanchoides Decne. ssp. **cynanchoides** (Decne.) R. Holm, stat. nov.

Sarcostemma cynanchoides Decne. in DC. Prodr. 8:540. 1844. (T.: *Berlandier 2324 in Herb. Paris*!).
Philibertia cynanchoides (Decne.) Gray, in Proc. Amer. Acad. 12:64. 1877.
Philibertia cynanchoides var. *subtruncatum* Robins. & Fern. in Proc. Amer. Acad. 30:119. 1894. (T.: *Hartmann 4 in Herb. U. S. Nat. Mus.*!).
Philibertella cynanchoides (Decne.) Vail, in Bull. Torr. Bot. Club 24:307. 1897.
Funastrum cynanchoides (Decne.) Schltr. in Fedde's Repert. 13:284. 1915.
Funastrum cynanchoides var. *subtruncatum* (Robins. & Fern.) Macbr. in Contr. Gray Herb. n. s. 49:51. 1917.

Stems twining or trailing, green to gray-green, glabrous to sparsely puberulent; lateral branches many. Leaves broadly ovate-lanceolate, acuminate to acute, cordate, rarely truncate or somewhat hastate, the lobes usually diverging, 2–3 cm. long, 0.5–3.0 cm. wide, membranaceous, sparsely puberulent on both surfaces, with one or more glands on the midrib at the base; petiole 0.9–1.5 cm. long. Inflorescences umbelliform, 12- to 20-flowered; peduncle 3.5–4.0 cm. long, glabrescent; bracts linear, minute; pedicels slender, 1.5–1.7 cm. long, minutely pilosulose. Calyx lobes ovate, 2–3 mm. long, pilosulose without, glabrous within; squamellae absent, solitary, or paired. Corolla rotate-subcampanulate, greenish-white, rarely pinkish, the tube 2 mm. long, the lobes ovate, acute, 6–7 mm. long, glabrescent without, glabrous within, more or less ciliolate. Gynostegium 2 mm. high, the column about 0.5 mm. long. Anthers 1 mm. long, the apical appendage suborbicular, the pollinium-sacs oblongoid-cylindrical, 0.6 mm. long, with sagittate corpusculum; ring of the corona thin, revolute, not adnate to the base of the corona vesicles; vesicles of the corona suboblongoid, widest above the middle, 1.5 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head convex, obscurely bilobed. Follicles fusiform, 6.5–7.2 cm. long, 1.0–1.3 cm. thick, puberulent, finely striate; seeds unequally biconvex, 7–8 mm. long, 3–4 mm. wide, minutely papillate on both surfaces, the margin serrate; coma about 3.5 cm. long.

As interpreted here, *Sarcostemma c. cynanchoides* represents the eastern subspecies of a species ranging from Oklahoma and central Texas to western Mexico and California. While it usually can be distinguished easily from the western subspecies by its broader, shorter leaves and white flowers, these differences do not appear to be sufficiently important for specific designation. *Sarcostemma c. cynan-*

choides occupies less arid habitats and shows less evidence of morphological reduction than its western relative. It also begins to flower nearly two months later. Floral differentiation between the two subspecies is not striking: S. *c. cynanchoides* has a somewhat longer column and the corona vesicles are widest above the middle in the majority of specimens. Hybridization between them appears to be rather rare (time of flowering may be a barrier), but the area of overlap of the two ranges is in Mexico where few specimens have been collected. The nature of the cline is further discussed in connection with *Sarcostemma c. Hartwegii* (10b).

Sarcostemma c. cynanchoides has been found climbing trees and shrubs in the sandy soil of rivers and ditches and in rocky canyons; it grows at altitudes of 1600 to 6400 feet. Blooming dates range from May to September and fruit have been collected in August and September.

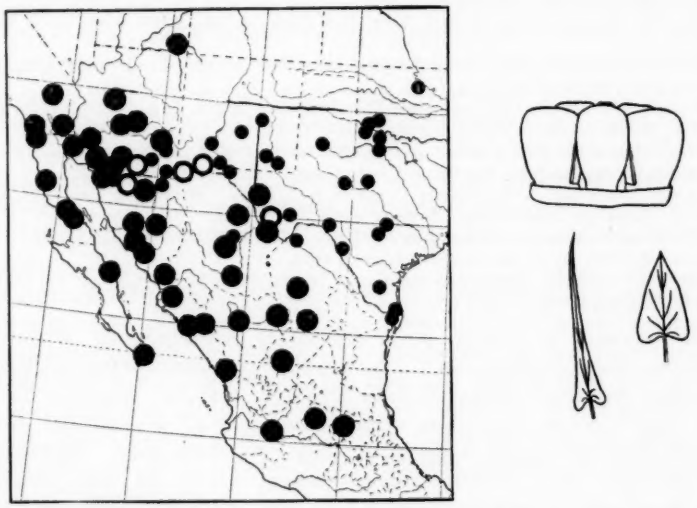

Fig. 13. Distribution of *S. cynanchoides cynanchoides* (small dots), of *S. cynanchoides Hartwegii* (large dots), of putative hybrids (black circles). Gynostegium of *S. cynanchoides* spp. (upper right); leaf of *S. cynanchoides Hartwegii* (lower left), of *S. cynanchoides cynanchoides* (lower right).

UNITED STATES. OKLAHOMA: COMANCHE CO.: Fort Sill, *Clemens 11734;* PAYNE CO.: Ripley, *Stratton 237;* TELLMAN CO.: S of Davidson, *Goodman 2266.* TEXAS: ARCHER CO.: Kickapoo Creek, *Reverchon 602;* BEXAR CO.: San Antonio, *Wilkinson s. n.;* BREWSTER CO.: Chisos Mts., *Tharp 3650;* BROWN CO.: Jim Ned Creek, *Reverchon s. n.;* CAMERON CO.: Brownsville, *Schulz 2094;* COMAL CO.: New Braunfels, *Lindheimer 993;* DUVAL CO.: Pena, *Nealley 375;* EL PASO CO.: El Paso, *Stearns 125;* HALL CO.: Estelline, *Reverchon 3875;* LUBBOCK CO.: Slaton, *Reed 3228;* MAVERICK CO.: Eagle Pass, *Havard s. n.;* TOM GREEN CO.: *Soulard s. n.;* VALVERDE CO.: Devil's River, *Eggert s. n.;* WILBARGER CO.: Vernon, *Ferris & Duncan 3352;* YOUNG CO.: Graham, *Reverchon 3199.* NEW MEXICO: CHAVES CO.: Roswell, *Earle & Earle 242;* DONA ANA CO.: Mt. Selden, *Rusby 261;* EDDY CO.: Dark Cañon, 45 miles SW of Carlsbad, *Grassl 98;* GUADALUPE CO.: Sta. Rosa, *Arsène & Benedict 16050;* LINCOLN CO.: above Tularosa, *Wooton & Standley s. n.;* LUNA CO.: Florida Mts., *Mulford 1041a;* SIERRA CO.: Animas Creek, *Metcalfe 1128.* ARIZONA: COCHISE CO.: Bisbee, *Mearns 879;* GRAHAM CO.: Clifton, *Hough s. n.;* PIMA CO.: Tucson, *Kearney & Peebles 14989.*

MEXICO. CHIHUAHUA: Rio Carmen, N of Chihuahua, *Wislizenus 105;* Paso del Norte, *Pringle 1324;* Sta. Eulalia Plains, *Wilkinson s. n.* COAHUILA: Matamoros, *Berlandier 2324,* type of *S. cynanchoides* Decne., *904, 2334;* Del Carmen Mts., *Marsh 840.* NUEVO LEON: El Carrizo, *Pringle 13117;* Rio Brazo del Norte, *Schott s. n.* SONORA: Fronteras, *Hartmann 4,* type of *P. c.* var. *subtruncatum* Robins. & Fern., *984, 985;* Guadalupe Canyon, *Merton 2053.*

10b. SARCOSTEMMA CYNANCHOIDES Decne. ssp. **Hartwegii** (Vail) R. Holm, stat. nov.

Sarcostemma lineare Decne. ex Benth. Pl. Hartw. 25. 1840, non Sprengel. (T.: *Hartweg 217*!).

Sarcostemma heterophyllum Engelm. sensu Torr. in Bot. Mex. Bound. Surv. 162. 1859, as to specimens cited, not as to type.

Philibertia linearis (Decne.) Gray, Proc. Amer. Acad. 12:64. 1877.

Philibertia linearis var. *heterophylla* (Engelm. sensu Torr.) Gray, Syn. Fl. 2^1:88. 1878, as to description, not as to type.

Philibertella Hartwegii Vail, in Bull. Torr. Bot. Club 24:308. 1897, based on *S. lineare* Decne.

Philibertella Hartwegii heterophylla (Engelm. sensu Torr.) Vail, loc. cit. 1897, as to specimens cited, not as to type.

Philibertella heterophylla (Engelm. sensu Torr.) Cocker. in Bot. Gaz. 26:279. 1898, based on *P. Hartwegii heterophylla* (Engelm. sensu Torr.) Vail.

Funastrum Hartwegii (Vail) Schltr. in Fedde's Repert. 13:285. 1914.

Funastrum lineare (Decne.) Macbr. in Contr. Gray Herb. n. s. 49:50. 1917.

Funastrum lineare var. *heterophyllum* (Engelm. sensu Torr.) Macbr. loc. cit. 1917, based on *P. Hartwegii heterophylla* (Engelm. sensu Torr.) Vail.

Funastrum heterophyllum (Engelm. sensu Torr.) Standl. in Contr. U. S. Nat. Herb. 23:1170. 1924, as to description, not as to type.

Philibertia heterophylla (Engelm. sensu Torr.) Jepson, Man. Fl. Pl. Calif. 770. 1925, as to description, not as to type.

Stems twining or trailing, green, glabrate to puberulent, the nodes white puberulent; lateral branches many. Leaves narrowly lanceolate, acuminate, hastate, or cordate, sometimes obtuse, the lobes diverging, 1–11 cm. long, 0.1–2.5 cm. wide, membranaceous, glabrate to subpuberulent on both surfaces, with one or more glands on the midrib at the base; petiole 0.9–1.9 cm. long. Inflorescences umbelliform, 7- to 14-flowered; peduncle slender, 0.5–5.5 cm. long, pilosulose; bracts linear, minute; pedicels slender, 0.7–1.5 cm. long, puberulent. Calyx lobes ovate-linear, 2–3 mm. long, pilosulose without, glabrous within; squamellae usually solitary. Corolla rotate-subcampanulate, purple to pink, or the lobes each with a median purple streak, the tube 1 mm. long, the lobes ovate, acuminate to acute, 5–7 mm. long, puberulent without, glabrous within, ciliolate. Gynostegium 2.5 mm. high, the column very short. Anthers 1 mm. long, the apical appendage suborbicular, the pollinium-sacs oblongoid-cylindrical, with ellipsoid-sagittate corpusculum; ring of the corona prominent, not adnate to the base of the corona vesicles; vesicles of the corona rectanguloid, widest below the middle, 1.5 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head convex, obscurely bilobed. Follicles slender, fusiform, attenuate, 7.4–11.0 cm. long, 0.6–1.0 cm. thick, minutely puberulent, finely striate; seeds unequally biconvex, 6 mm. long, 1.5 mm. wide, minutely rugose dorsally, minutely papillate ventrally; coma about 3.5 cm. long.

The taxonomy of this subspecies and of S. *crispum* is confused by the widespread misapplication of the name S. *heterophyllum* Torr. In 1859, Torrey published this manuscript name of Engelmann, citing but one specimen, *Wright 1679*, which must be regarded as the type. This specimen, however, is an example of S. *crispum* with very narrow leaves in which crisping or undulation is not apparent. Two years later, Torrey referred *Wright 1681* of the Mexican Boundary Survey collections to S. *heterophyllum*. This specimen proves to be S. *cynanchoides Hartwegii* and the description given by Torrey clearly applies to that subspecies. All later authors have followed this misapplication of the name in making various combinations in *Philibertia*, *Philibertella*, and *Funastrum*.

Inasmuch as the type of the first-published S. *heterophyllum* actually is S. *crispum*, this name and subsequent combinations are nomenclaturally related to S. *crispum* and unavailable for the lanceolate-leaved subspecies of S. *cynanchoides*. The epithet *lineare* also is pre-empted by the earlier name of Sprengel. I have preferred to employ *Hartwegii*, rather than coin a new name, despite the fact that, owing to this early misunderstanding, it never was used widely.

Sarcostemma c. Hartwegii is similar to the eastern subspecies in most respects, differing in the narrower, longer leaves and purple flowers. Intergradation between the two forms appears to be uncommon, but occurs in a narrow northwest-southeast belt from Arizona to central Mexico. Hybridization has produced an abruptly stepped cline and intermediate forms have been designated as S. *c.* cl. *cynanchoides-Hartwegii*.

In contradistinction to S. *c. cynanchoides*, S. *c. Hartwegii* usually grows in dry, sandy or rocky soil of arroyos and plains. Occasionally it is found in cultivated bottom lands and ditches, in which case the flowers are larger and the leaves often fully ten times as large as normal. The altitudinal range is from 100 to 5000 feet, overlapping that of the eastern subspecies. Flowering specimens have been collected from February to early September, this season beginning about two months before that of S. *c. cynanchoides*. Fruiting specimens dated from April to October have been seen.

UNITED STATES. UTAH: SAN JUAN CO.: 6 miles above mouth of San Juan River, *Cutler 3180*; Forbidding Canyon, near Colorado River, *Cutler 2831*. TEXAS: BREWSTER CO.: Chisos Mts., *Muller 8117*; CULBERSON CO.: near Van Horn, *Waterfall 5447*; PRESIDIO CO.: Presidio, *Havard s. n.* NEW MEXICO: DONA ANA CO.: mesa W of Organ Mts., *Standley s. n.*; LUNA CO.: Florida Mts., *Mulford 1063*. ARIZONA: GILA CO.: Collom Camp, Matzatzal Mts., *Collom 6*; GRAHAM CO.: near Safford, *Maguire 10931*; PIMA CO.: near Sta. Rosa, *Cutler 4724*; PINAL CO.: near Mammoth, *Peebles 14611*; MARICOPA CO.: 23 miles N of Phoenix, *Gillespie 8660*; YAVAPAI CO.: near Congress Junction, *Gillespie 8502*. CALIFORNIA: IMPERIAL CO.: near Ogilby, *Alexander & Kellogg 1951*; LOS ANGELES CO.: Covina, *G. B. Grant 972*; RIVERSIDE CO.: Snow Creek Canyon, San Jacinto Mts., *Munz 12397*; SAN BERNARDINO CO.: San Bernardino Valley, *Parish & Parish 309*; SAN DIEGO CO.: Box Canyon, *Munz & Hitchcock 12048*.

MEXICO. BAJA CALIFORNIA NORTE: Punta Prieta, *Wiggins 7738*; 30 miles N of Punta Prieta, *Wiggins 5346*; San Quintín Bay, *E. Palmer 639*; 14.5 miles E of Agua Caliente, *Keck 1925*. BAJA CALIFORNIA SUR: Mulege, *Johnston 3684*; Santa Agueda, *E. Palmer 231*; near San José del Cabo, *Wiggins 5682*. CHIHUAHUA: Bachimpa, S of Chihuahua, *Wislizenus 255*; near Chihuahua, *E. Palmer 84*, *Pringle 1051*; Sta. Eulalia Plains, *Wilkinson*

s. n.; 5 miles E of Allende turn-off, road Parral-Camargo, *Freytag & Baxter 65*. COAHUILA: Movans, *Purpus 4485*; 10 miles N of Cuatro Ciénegas, *Wynd 738*; near Parras, *Shreve 8761*; Torreon, *Pittier 505*. DURANGO: Santiago Papaquiaro, *Nelson 4661*, *E. Palmer 39*. GUANAJUATO: Guanajuato, *Duges 7*. JALISCO: near Guadalajara, *Pringle 5885*, *8497*, *11628*, *Safford 1426*. QUERÉTARO: near San Pablo, *Rose, Painter & Rose 9817*; between Huiguerilla and San Pablo, *Altamirano 7702*. SINALOA: San Blas, *M. E. Jones 23249*; Villa Union, *Lamb 445*; Altata, *Rose 1375*; Culiacán, *Partidas 2015*, *2016*; San Ignacio, *Montes & Salazar 53*; near Fuerte, *Rose, Standley & Russell 13928*; near Villa Union, *Rose, Standley & Russell 14639*. SONORA: Cocorit, Yaqui Valley, *Gentry 888*; San Bernardo, Rio Mayo, *Gentry 1308*; 5.7 miles NW of Caborca, *Wiggins 8265*; near Suhuoral, *Wiggins & Rollins 264*; 24 miles SW of Sonoyta, *Shreve 7588*; 35.3 miles SW of Sonoyta, *Wiggins 8363*; near Guaymas, San Carlos Bay, *Ferris 8730*; Rancho San Ignacio, 10 miles N of Vicam, *Wiggins 6461*; Forin, *Studhalter 1370*; near Cucurpe, *Wiggins 7170*; Hermosillo, *Maltby 198*; Alamos, *Goldman 307*; Pitequito, *Kennedy 7080*, *Keck 4014*; near Altar, *Long 10*; near Magdalena, *Rose, Standley & Russell 15065*; Realito, 10 miles E of Altar, *Shreve 6371*; Navajoa, *Rose, Standley & Russell 13134*; 20 miles N of Sargento, *Mallery & Turnage s. n.* ZACATECAS: Cedros, *Lloyd 123*.

SARCOSTEMMA CYNANCHOIDES cl. CYNANCHOIDES-HARTWEGII.

UNITED STATES. TEXAS: PRESIDIO CO.: 24 miles S of Marfa, *Hinckley 1051*. NEW MEXICO: HIDALGO CO.: Virdin, *Hershey A-11*; LUNA CO.: Florida Mts., *Mulford 1041a*. ARIZONA: PIMA CO.: Rincon Mts., *Harrison & Kearney 5820*.

MEX.CO. SONORA: along Río de los Alisos, 31 miles S of Nogales, *Wiggins 7034A*.

11. SARCOSTEMMA **hirtellum** (A. Gray) R. Holm, comb. nov.

Sarcostemma heterophyllum Engelm. sensu Torr. var. *hirtellum* Gray, in Brewer & Watson, Bot. Calif. 1:178. 1876. (T.: *Cooper s. n.*!).
Philibertia linearis (Decne.) Gray, var. *hirtella* Gray, Syn. Fl. 2^1:88. 1878.
Philibertella hirtella (Gray) Vail, in Bull. Torr. Bot. Club 24:309. 1897.
Philibertia hirtella (Gray) Parish, in Muhlenbergia 3:126. 1907.
Funastrum hirtellum (Gray) Schltr. in Fedde's Repert. 13:286. 1915.

Stems twining, trailing, or semi-erect, gray-green, densely canescent; lateral branches many. Leaves linear to narrowly lanceolate, acuminate to acute, obtuse, rarely truncate, 1.0–3.6 cm. long, 0.1–0.5 cm. wide, pilosulose on both surfaces, coriaceous, without glands on the midrib; petiole 0.1–1.5 cm. long. Inflorescences umbelliform, 9- to 12-flowered; peduncle 1.5–4.9 cm. long, pilosulose; bracts linear, minute; pedicels 0.6–0.9 cm. long, pilosulose. Calyx lobes linear, 2.0–2.5 mm. long, densely subpilose on both surfaces; squamellae absent or solitary. Corolla rotate-subcampanulate, white, the tube 1 mm. long, the lobes ovate-lanceolate, acute, 4–5 mm. long, glabrous without, subpilose within, ciliolate. Gynostegium 2 mm. high, the column about 0.5 mm. long. Anthers 0.75 mm. long, the apical appendage ovate-elliptic, the pollinium-sacs somewhat flattened, 0.5 mm. long, with ellipsoid to narrowly sagittate corpusculum; ring of the corona thin, adnate to the base of the corona vesicles; vesicles of the corona oblongoid, 1.5 mm. long. Ovaries 1.5 mm. long, essentially glabrous; stigma-head slightly convex, obscurely bilobed. Follicles paired, narrowly fusiform, grayish-yellow, waxy, 3.8–4.7 cm. long, 0.3–0.5 cm. thick, very minutely but thickly puberulent; seeds somewhat flattened, 8 mm. long, 4 mm. wide, rugose-papillate dorsally, minutely papillate ventrally; coma about 2.5 cm. long.

Sarcostemma hirtellum has a restricted distribution in the Colorado and Mojave deserts in Nevada, California, and Arizona. It has been confused in the herbarium with S. *cynanchoides Hartwegii* from which it differs in the narrow, pubescent leaves, canescent aspect, and semi-erect habit, in addition to important, though less prominent, floral differences. In contradistinction to all other species in the New World, S. *hirtellum* appears invariably to have paired follicles which diverge markedly from one another. The species probably is most closely related to the western subspecies of S. *cynanchoides*, but must be considered a species on morphological criteria.

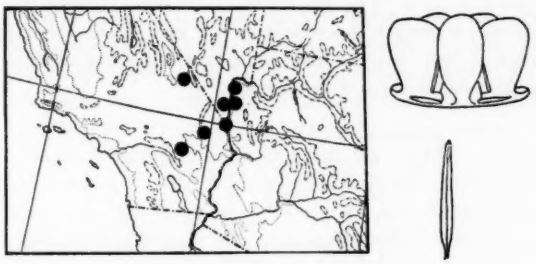

Fig. 14. Distribution, gynostegium, and leaf of S. *hirtellum*.

Sarcostemma hirtellum occurs at altitudes of from 450 to 3500 feet. It is an undershrub several feet in height, but creeping branches may extend several feet along the sandy or rocky soil of the ravines of washes in which it grows. While the aerial stems are slender and herbaceous, there is a large, woody caudex at the base and a series of very stout, deeply penetrating roots. The crushed herbage has an odor pronouncedly sudoral or reminiscent of garlic. Blooming dates range from March 26 to May 5; one specimen was collected in flower in October. Follicles are produced from April to May.

UNITED STATES. NEVADA: CLARK CO.: 14 miles E of Searchlight, *Train 1283;* Mike Tobins, *Thackery 333.* ARIZONA: MOHAVE CO.: 7 miles S of Boulder Dam, *Peebles & Parker 14785;* YUMA CO.: Buckskin Mts., *Keck 4345.* CALIFORNIA. CALAVERAS CO.: Vallecito, *Orcutt 2250;* RIVERSIDE CO.: Corn Springs, *C. L. Hitchcock 12199;* SAN BERNARDINO CO.: near Needles, *Macbride & Drouet 4453;* SAN DIEGO CO.: San Felipe Canyon, *Eastwood 2780.*

12. SARCOSTEMMA ARENARIUM Decne. ex Benth. Bot. Voy. Sulph. 34. 1844. (T.: *Hinds 1841 in Herb. Kew.*!).

Stems twining or trailing, very thick at the base and with much ridged bark, gray-green above, puberulent, the nodes densely white-pubescent; lateral branches many and long at the base, few above. Leaves more or less caducous, narrowly oblanceolate, obtuse, cuneate, 3.5 cm. long, 0.3–0.8 cm. wide, coriaceous, somewhat revolute when dried, sparsely pilose above and beneath with small glands on the midrib at the base; petiole 0.05–0.1 cm. long. Inflorescences umbelliform, 6- to 12-flowered; peduncle 2.2–3.5 cm. long, rarely equalling the subjacent inter-

node in thickness, pilose; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–1.3 cm. long, densely pilose. Calyx lobes narrowly lanceolate, 3 mm. long, involute, pilose without, glabrous within; squamellae alternate, usually solitary, relatively long. Corolla rotate-subcampanulate, the tube 2.5–3.0 mm. long, the lobes ovate, obtuse, 4.5–6.0 mm. long, pilose without, puberulous-papillate within, ciliate. Gynostegium 2.5–3.0 mm. high, the column 1 mm. long. Anthers 1 mm. long, the apical appendage deltoid, the pollinium-sacs clavate-oblongoid, 0.5 mm. long, with narrowly sagittate corpusculum; ring of the corona prominent, somewhat revolute, adnate to the column; vesicles of the corona spherical to oblongoid, 1.0–1.5 mm. long. Ovaries 2 mm. long, rather densely pilose; stigma-head obscurely bilobed, convex. Follicles narrowly obclavate, attenuate, 6.4 cm. long, 0.9 cm. thick, puberulent; seeds unequally biconvex, 7 mm. long, 3 mm. wide, obscurely rugose dorsally, minutely papillate ventrally; coma about 3 cm. long.

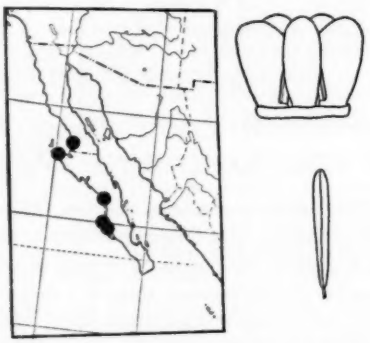

Fig. 15. Distribution, gynostegium, and leaf of *S. arenarium*.

A poorly understood species endemic to the western coast of Baja California. *Sarcostemma arenarium* has been confused with *S. cynanchoides Hartwegii* and *S. hirtellum*, from both of which, however, it is rather easily distinguished by its oblanceolate leaves, larger flowers, and densely pubescent calyx. In many respects it is fairly close to *S. clausum*, and may perhaps represent an offshoot of that variable stock. If so, it has diverged so far in the direction of ser. CYNANCHOIDES as to make any statements concerning its relationships very tenuous.

MEXICO. BAJA CALIFORNIA SUR: San Bartolomé Bay, *Rose 16214*; Magdalena Bay, *Mason 1929*, *Hinds 1841*, TYPE; Magdalena Island, *Orcutt 31*, *Brandegee 1889*; Lagoon Head, *E. Palmer 814*; San Juanico, *Gentry 4297*.

Series 4. ANGUSTISSIMA R. Holm, ser. nov.

Inflorescentia vere terminalis umbelliformis, pedunculo quam internodio subjacenti angustiore (interdum obsoleto).

Type species: *Sarcostemma angustissimum* (Anderss.) R. Holm.

This monotypic series includes a single species, endemic to the Galapagos Islands, which differs from other members of the genus in having a truly terminal inflorescence.

13. SARCOSTEMMA **angustissimum** (Anderss.) R. Holm, comb. nov.

Asclepias angustissima Anderss. Galap. Oarnes Veg. 196. 1853. (T.: *Andersson s. n. in Herb. Stockholm*!).
Funastrum angustissimum (Anderss.) Fourn. in Ann. Sci. Nat. Bot. VI, 19:388. 1882.

Stems twining or semi-erect, green, glabrous; lateral branches many. Leaves oblanceolate, linear, acute, cuneate, 2.5–4.5 cm. long, 0.1–0.3 cm. wide, subcoriaceous, revolute when dried, glabrous above and beneath, without glands on the midrib at the base; petiole 0.1–0.2 cm. long. Inflorescences umbelliform, terminal to the main axis or lateral branches, 7- to 15-flowered; peduncle 0–1 cm. long, very minutely pilosulose, not equalling the subjacent internode in thickness; bracts linear, minute; pedicels 0.5–1.5 cm. long, very minutely pilosulose. Calyx lobes ovate, 1.5 mm. long, hispidulous without, glabrous within, ciliolate, the apex glandular; squamellae absent. Corolla rotate-subcampanulate, black when dried, the tube 1.25 mm. long, the lobes ovate, acute, 2.5 mm. long, glabrous on both surfaces. Gynostegium 2 mm. high, the column very short. Anthers 1 mm. long, the apical appendage semi-orbicular, the pollinium-sacs oblongoid, 0.5 mm. long, with sagittate corpusculum; ring of the corona thin, scarcely adnate to the base of the corona vesicles; vesicles of the corona ovoid-oblongoid, pointed at the tip, 2 mm. long. Ovaries 1 mm. long, very minutely pubescent; stigma-head convex, entire. Follicles apparently narrowly fusiform, about 9 (?) cm. long; seeds unknown.

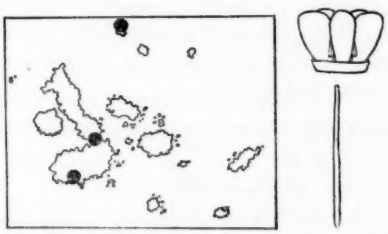

Fig. 16. Distribution, gynostegium, and leaf of *S. angustissimum*.

The small, dark flowers of this Galapagos Island endemic are quite distinctive, as are the terminal inflorescences. Little can be said about the relationships of *S. angustissimum* since it has been so rarely collected and is so reduced morphologically. Apparently it flowers from January to June.

GALAPAGOS ISLANDS. ABINGDON IS.: *Snodgrass & Heller 845*. ALBEMARLE IS.: *Andersson s. n.*, TYPE; Tagus Cove, *Snodgrass & Heller 145*.

Series 5. FLAVA R. Holm, ser. nov.

Coronae annulus obsoletus.

Type species: *Sarcostemma flavum* Decne.

A monotypic series including a species of the Río de la Plata area of South America. The ring of the corona is entirely lacking, immediately separating this species from all others in the subgenus.

14. SARCOSTEMMA FLAVUM Decne. in DC. Prodr. 8:540. 1844. (T.: *D'Orbigny s. n. in Herb. Paris.*!).

Philibertia stellaris Griseb. Symb. Fl. Arg. 234. 1879, ex char.
Cystostemma umbellatum Fourn. in Mart. Fl. Bras. 6^4:204. 1885. (T.: *St. Hilaire s. n.*!).
Ceramanthus flavus (Decne.) Malme in Ark. Bot. 4^{14}:2. 1905.
Philibertia longifolia Arech. in Ann. Mus. Nac. Montevideo 4:87. 1909, ex char.
Funastrum flavum (Decne.) Malme, in Bull. Soc. Bot. Genève. II, 3:269. 1911.
Funastrum longifolium (Arech.) Schltr. in Fedde's Repert. 13:286. 1915.

Stems twining, green, pilosulose; lateral branches few. Leaves long, lanceolate, acuminate to acute, cordate, the lobes descending, 7.0–12.5 cm. long, 3.5–4.0 cm. wide, subcoriaceous, appressed-pilose above, densely so beneath, with several glands on the midrib at the base; petiole 1.5–2.0 cm. long. Inflorescences umbelliform, the floriferous axis slightly manifest, 9- to 15-flowered; peduncle 4.5–14.0 cm. long, pilosulose; bracts linear, minute; pedicels 5–10 cm. long, pilose. Calyx lobes narrowly lanceolate, 2.5 mm. long, copiously puberulent without, glabrous within; squamellae 3–7, alternate. Corolla rotate-subcampanulate, the tube 0.9 mm. long, the lobes broadly ovate, 4 mm. long, glabrescent without, glabrous within. Gynostegium 2.5 mm. high, the column obsolete. Anthers 1.5 mm. long, the apical appendage deltoid, obscurely emarginate, the pollinium-sacs oblongoid-cylindrical, 0.5 mm. long, with ellipsoid to obscurely sagittate corpusculum; ring of the corona lacking; vesicles of the corona ovoid, the inner side more or less apiculate at the tip, 2.5 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head obscurely bilobed. Follicles and seeds unknown.

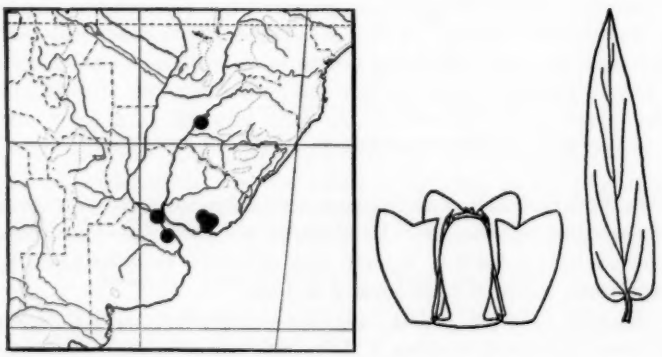

Fig. 17. Distribution, gynostegium, and leaf of *S. flavum*.

This distinctive species apparently is rare, for few specimens have been available for study. The lack of the ring of the corona and the disproportionate length of the leaves form good characters. One of the few species which occurs in lowland areas, it inhabits the borders of the Paraná and Plata rivers. Only the type specimen and the material from the Naturhistoriska Riksmuseet, Stockholm, have been available, so that most of the distribution records are taken from the monograph of the Argentine species of *Funastrum* and *Philibertia* by T. Meyer.[56] The species ranges from southern Brazil to adjacent Argentina and Uruguay.

BRASIL. RÍO GRANDE DO SUL: *St. Hilaire s. n.*, type of *C. umbellatum* Fourn.
URUGUAY. CANELONES: near the Río de la Plata, *Legrand 34*. CERRO LARGO: Cerro de las Cuentas, *Rosengurtt 2773*. SAN JOSÉ: Barra, *Herter 738*; Santa Lucía, *Arechaveleta s. n.*
ARGENTINA. BUENOS AIRES: Conchitas, orillas del Río de la Plata, *Hauman s. n.*; delta del Paraná, *Hauman s. n.* ENTRE RÍOS: Río Bravo, *Kuschel 532, 533, 534*.

Subgenus II. OXYSTELMA (R. Br.) R. Holm, stat. nov.

Oxystelma R. Br. in Mem. Wern. Soc. 1:40. 1809.
Philibertia HBK. Nov. Gen. et Sp. Pl. 3:195. 1819.
Pentagonium Schauer, in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.
Lugonia Wedd. Chlor. And. 2:49. 1857.
Zosima Phil. Sert. Mend. Alt. 29. 1871, non Hoffm.
Pentacyphus Schltr. in Engl. Bot. Jahrb. 37:605. 1906.
Tetraphysa Schltr. loc. cit. 616. 1906.

Leaves laminate; inflorescences racemiform or umbelliform; corolla subrotate-campanulate to campanulate, ring of the corona adnate to the corolla or more or less obsolete.

Type species: *Sarcostemma esculentum* (L.) R. Holm.

The species of this subgenus are South American plants of Andean affinities, except for the Old World *S. esculentum* which occurs in Africa and Asia. Because of the close similarity in vegetative structure between the various species, it has been necessary to place a greater emphasis on characters of the gynostegium in the keys. In every case, however, examination of the dried flowers should suffice for identification; drawings are provided to illustrate the typical condition for each species.

KEY TO THE SECTIONS

A. Vesicles of the corona ovoid to subspheroid, obtuse at the apex or abruptly constricted to form a short apical process, never exceeding the stigma-head in length; ring of the corona glabrous or obsolete; column glabrous; translator arms well-developed. Species of the Western Hemisphere.
B. Corolla lobes acute or acuminate, the tube free from the column (partly adnate in *S. lysimachioides*), glabrous within; gynostegium not highly vernicose, the column terete or ribbed, not deeply grooved; inflorescences racemiform or umbelliform, consisting of many 1- to 2-flowered cymules (occasionally indicated only by their bracts or reduced to one).....Section 1. PHILIBERTIA (Spp. 15–20)

[56] Meyer, T. In Lilloa 9:428. 1943.

BB. Corolla lobes broadly obtuse, the tube adnate to the column directly below the anthers, pubescent within forming five hairy pouches alternating with the stamens; gynostegium highly vernicose, the column longitudinally grooved between the stamens, the margins of the groove produced and arrect, continuous with the anther wings; inflorescence racemiform, consisting of 2 1-flowered cymules, or umbelliform. ..... Section 2. PENTACYPHUS (Spp. 21–22)

AA. Vesicles of the corona ovoid, gradually constricted above into a long, incurved process, exceeding the stigma-head in length; ring of the corona pubescent; column pubescent; translator arms obsolete. Species of the Eastern Hemisphere..... Section 3. EUOXYSTELMA (see p. 482)

Section 1. PHILIBERTIA (HBK.) Decne. in DC. Prodr. 8:541. 1844.

The majority of the species in the subgenus OXYSTELMA belong to this group of forms of undoubted close relationship. All appear to be more or less localized in distribution, in contrast to the species of subg. CERAMANTHUS or EUSARCOSTEMMA, except for *S. Gilliesii* of Argentina and Bolivia. As a rule, they may be recognized easily by the campanulate corolla, the glabrous gynostegium with scarcely apparent corona ring, and the few-flowered inflorescence.

KEY TO THE SPECIES

a. Plants usually climbing, very rarely semi-erect; corolla tube free from the column.

b. Corolla broadly and shallowly campanulate; vesicles of the corona equalling or somewhat exceeding the anthers (rarely reduced in aberrant individuals, cf. *S. Gilliesii*); pollinia rounded, clavate-cylindrical, fertile to the attachment of the translator arm, the corpusculum sagittate.

c. Vesicles of the corona narrowly ovoid-oblongoid, with a vertical ventral keel, gradually decurrent upon the column, the gynostegium somewhat longer than broad; sepals reflexed, corolla 2–3 cm. broad..... 15. *S. campanulatum*

cc. Vesicles of the corona truncate-oblongoid or ovoid to spheroid, not decurrent upon the column, the gynostegium usually broader than long; sepals ascending, corolla 0.8–1.0 cm. broad, rarely to 2 cm. broad.

d. Inflorescences racemiform to corymbiform, obviously compound; stigma-head usually 2-apiculate; vesicles of the corona narrowly ovoid or obovoid to subspheroid, with a more or less pronounced apical appendage, constricted at their insertion upon the column.

e. Vesicles of the corona widest below the middle, the gynostegium uniformly light in color; corolla with purple markings within..... 16. *S. Gilliesii*

ee. Vesicles of the corona widest above the middle, light in color, the column and anthers very dark; corolla usually uniformly light in color..... 17. *S. Vaileae*

dd. Inflorescences umbelliform, the pedicels all inserted at nearly the same point; stigma-head umbonate or broadly 2-lobed; vesicles of the corona truncate-oblongoid, scarcely constricted at their insertion upon the column..... 18. *S. solanoides*

bb. Corolla urceolate-campanulate; vesicles of the corona about one-third to one-half the length of the anthers; pollinia flattened, clavate, with a sterile hyaline region at the attachment of the translator arm, the corpusculum narrowly ellipsoid..... 19. *S. stipitatum*

aa. Plants prostrate, the branches trailing from a short woody caudex; corolla tube adnate to the column directly below the anthers..... 20. *S. lysimachioides*

15. SARCOSTEMMA CAMPANULATUM Lindl. Bot. Reg. n.s 9, *t. 36.* 1846. (T.: *Hort. Veitch. in Herb. Univ. Cantab.*!).

Philibertia campanulata (Lindl.) Nichols. Dict. Gard. 3:96. 1886.
Philibertia hypoleuca Schltr. in Oesterr. Bot. Zeitschr. 45:450. 1895. (T.: *Kunze s. n. in Herb. Berol.*).
Philibertia splendens Lillo, in Physis 4:429. 1919. (T.: *Lillo 7350 in Herb. Lillo*!).
Philibertia speciosa Malme, in Ark. Bot. 26A[4]:32. 1935, *sphalm.*

Stems twining, minutely pilosulose in lines decurrent from the petioles; lateral branches few. Leaves lanceolate, acuminate, rather deeply cordate, the lobes descending, 3.5–8.0 cm. long, 1.0–4.8 cm. wide, firmly membranaceous, glabrate to minutely puberulent above, subtomentose to tomentose beneath, with one or more glands on the midrib at the base; petiole 1.0–4.2 cm. long. Inflorescences racemiform, 2- to 9-flowered; peduncle 0.7–7.8 cm. long, appressed-pilosulose; bracts linear, 0.2–0.3 cm. long; pedicels 1.1–2.4 cm. long, appressed-pilosulose. Calyx lobes narrowly lanceolate, reflexed, 4 mm. long, puberulous-pilose on both surfaces; squamellae few, alternate. Corolla campanulate, greenish yellow to cream with red or purple spots or streaks within, the tube 8 mm. long, the lobes acute to acuminate, 5 mm. long, pilosulose without, glabrous within. Gynostegium 5–6 mm. high, the column 2 mm. long. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs clavate-cylindrical, 0.5 mm. long, with broadly sagittate corpusculum; ring of the corona very short; vesicles of the corona narrowly oblongoid, the ventral face constricted longitudinally to form a vertical keel, gradually decurrent upon the column, 2 mm. long (rarely much reduced). Ovaries 2 mm. long, sparsely puberulent; stigma-head cylindrical, with a long 2- or 3-fid apiculation. Follicles and seeds unknown.

Sarcostemma campanulatum is distinguished from all other species of the genus by the structure of the gynostegium. Here the corona vesicles are constricted longitudinally along the ventral face so that a vertical ventral keel is produced; there is no terete appendage such as is found in many species. Dorsally, the corona vesicles are decurrent upon the column to the corolla. It is noteworthy that the anther wings are usually broad and cartilaginous, while the pollinia are stout and short and connected by broad, sagittate corpuscula. A peculiar variant, which has been collected several times in the Cuzco region in Peru, has corona vesicles which are shrunken and more or less linear in outline. The gynostegium nevertheless is clearly that of S. *campanulatum*. As a rule in this form, the leaves are decidedly more tomentose beneath and the sepals are less strongly reflexed.

It is by virtue of the long, racemiform inflorescence and relatively unbranched habit, coupled with the large size, that S. *campanulatum* is assigned the primary position in the section. The relationships in subg. OXYSTELMA are, in general, much less clear than those in subg. CERAMANTHUS, so that this position in the sequence of species is based primarily on the general impression given by the plant, rather than upon any rigorous or dogmatic treatment of morphological criteria.

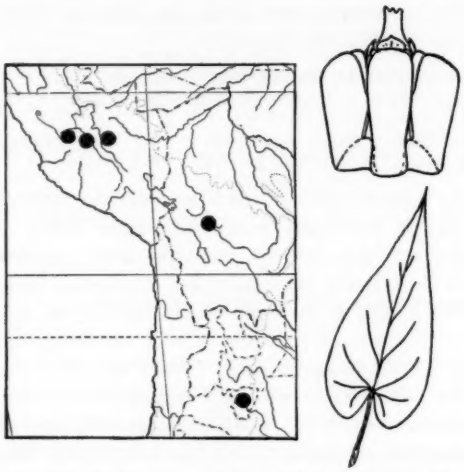

Fig. 18. Distribution, gynostegium, and leaf of S. *campanulatum*.

Sarcostemma campanulatum is a stout vine climbing to heights of four meters in small trees and shrubs. Apparently it grows in relatively moist locations in woods and occasionally in cultivated ground, at altitudes from 6000 to 11000 feet in the Peruvian and Bolivian Andes. The specimens from Tucumán, Argentina, are rather inexplicable. The species has been collected in flower from December to March, and in fruit in April.

Peru. apurimac: Abancay, Labrama, Matara Canyon, *Vargas 9801;* Abancay, Ampuy, *Stork, Horton & Vargas 10953;* Abancay, Labrama, *Vargas 1426;* Abancay, Mariño, *Vargas 1459.* cuzco: Anta, *Vargas 204;* Colca, Vilcabamba, *Vargas 4013;* Paruro, entre Huachachacca i Huanca-Huanca, *Vargas 2387.* huancavelica: Tayacaja, Ampurco, *Weberbauer 6503;* Tayacaja, 3 km. N of Salcabamba, *Stork & Horton 10318.*

Bolivia. cochabamba: Tunari, *Kuntze s. n.*, type of *P. hypoleuca* Schltr.

Argentina. tucumán: Tafí, La Angostura, *Castillón 2034;* Chicligasta, Estancia Las Pavas, *Venturi 6458.*

16. Sarcostemma Gilliesii (H. & A.) Decne. in DC. Prodr. 8:542. 1844.

Philibertia Gilliesii Hook. & Arn. in Hook. Lond. Jour. Bot. 1:290. 1834. (T.: *Tweedie s. n. in Herb. Kew.*!).

Philibertia grandiflora Hook. in Bot. Mag. 64, *t. 3618.* 1837. (T.: *Tweedie s. n. in Herb. Kew.*!).

Philibertia gracilis D. Don in Sweet, Brit. Fl. Gard. II, 4: *t. 403.* 1838. (T.: *Tweedie s. n. in Herb. Kew.*).

Sarcostemma Donianum Decne. loc. cit. 1844.

Sarcostemma grandiflorum (Hook.) Decne. loc. cit. 1844.

Sarcostemma incanum Decne. loc. cit. 1844. (T.: *D'Orbigny 246 in Herb. Paris*!).

Amblystigma pedunculare Benth. in Hook. Ic. Pl. 32:77. 1846. (T.: *Mandon 353 in Herb. Kew.*!).

Zosima violacea Phil. Sert. Mend. Alt. 29. 1871. (T.: *Philippi s. n.*!).

Oxystelma Gilliesii (H. & A.) K. Schum. in E. & P. Natür. Pflanzenfam. 4^2:229. 1895.

Oxystelma violacea (Phil.) K. Schum. loc. cit. 1895.

Philibertia Gilliesii H. & A. var. *pubescens* Speg. in Anal. Soc. Cient. Argent. 53:72. 1902, ex char. (T.: *Spegazzini s. n.*).
Philibertia violacea (Phil.) Schltr. in Fedde's Repert. 13:283. 1915.
Philibertia Gilliesii H. & A. var. *albida* Stuck. ex Seckt. Rev. Univ. Nac. Córdoba 17^{5-6}:70. 1930, ex char.
Philibertia Gilliesii H. & A. var. *vestita* Malme, Ark. Bot. $26A^{4}$:36. 1934, ex char.
Philibertia grandiflora Hook. f. *albida* Malme, loc. cit. 34. 1934, ex char. (T.: *Stuckert 13822 in Herb. Lillo*).
Philibertia Gilliesii H. & A. var. *grandiflora* (Hook.) T. Meyer, in Lilloa 9:452. 1943.
Philibertia Gilliesii H. & A. var. *gracilis* (D. Don) T. Meyer, loc. cit. 1943.
Philibertia Gilliesii H. & A. var. *parvicoronata* T. Meyer, loc. cit. 453. 1943. (T.: *Meyer 4117 in Herb. Lillo*!).
Philibertia Schreiteri T. Meyer, loc. cit. 436. 1943. (T.: *Schreiter 4540 in Herb. Lillo*!).
Philibertia Gilliesii H. & A. var. *mirabilis* T. Meyer, in Descole, Gen. et Sp. Pl. Argent. 2:173. 1944. (T.: *Meyer 5112 in Herb. Lillo*!).

Stems twining to rarely semi-erect, minutely puberulent in lines decurrent from the petioles; lateral branches many. Leaves narrowly lanceolate to ovate, acuminate to acute, deeply cordate, the lobes descending to converging, 2.5–4.0 cm. long, 0.3–3.2 cm. wide, membranaceous, revolute, glabrate to rather densely pilose on both surfaces, with one or more glands on the midrib at the base; petiole 1.0–2.5 cm. long. Inflorescences racemiform, 2- to 7-flowered; peduncle 1–5 cm. long, minutely puberulent; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–2.5 cm. long, minutely puberulent. Calyx lobes narrowly lanceolate, 2.5 mm. long, pilosulose without, glabrous within; squamellae alternate and few, or many and indefinitely distributed within the calyx. Corolla campanulate, greenish yellow to cream with red or purple spots or streaks within, the tube 6–9 mm. long, the lobes acute to acuminate, 1.5–2.0 mm. long, glabrous to pilosulose without, glabrous within. Gynostegium 3 mm. high, the column 1 mm. long. Anthers 1.0–1.5 mm. long, the apical appendage rhomboidal, the pollinium-sacs clavate-cylindrical, 0.5 mm. long with sagittate corpusculum; ring of the corona obsolete; vesicles of the corona ovoid to subspheroid, abruptly constricted at the apex to form a more or less pronounced apiculation, abruptly constricted at their insertion upon the column, 1.5 mm. long. Ovaries 2 mm. long, glabrous; stigma-head cylindrical, 2-apiculate, the apiculae often flattened and reflexed. Follicles about 3.5 cm. long, 0.7 cm. thick; seeds unknown.

In many respects *Sarcostemma Gilliesii* is the counterpart, in subg. OXYSTELMA, of *Sarcostemma* (CERAMANTHUS) *clausum*. I have considered it to be a polytypic species which has developed a number of races, apparently in response largely to increasing aridity. These populations, however, do not appear to be sufficiently distinct to be classified even as subspecies and therefore are not recognized nomenclaturally. The element known as *Philibertia gracilis* is, for the most part, northern (Bolivia and adjacent Argentina), and is a slender vine with broad, cordate, membranaceous, and glabrous leaves. In the southern provinces of Argentina is the so-called variety *pubescens* of *P. Gilliesii*, with narrow, hastate, subcoriaceous, and densely pubescent leaves. More or less intermediate geographically and morphologically (but broadly overlapping at both extremes) is the typical *S. Gilliesii*.

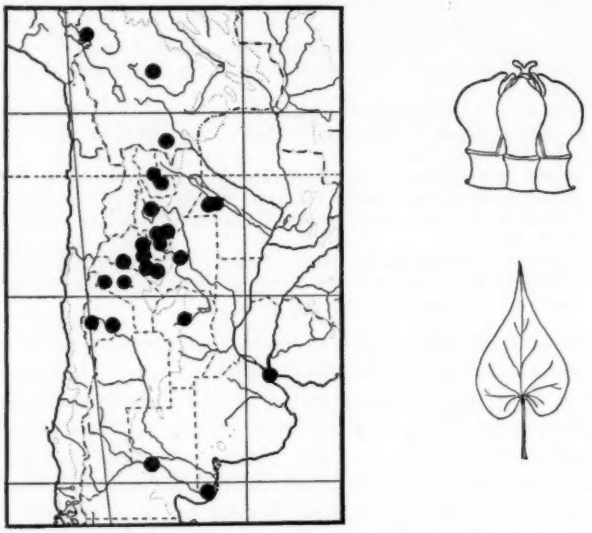

Fig. 19. Distribution, gynostegium, and leaf of *S. Gilliesii*.

There are also several local variants which are of interest: var. *parvicoronata* of T. Meyer includes those relatively common, but by no means distinct, forms in which the corona vesicles are shrunken and linear in outline; *P. Schreiteri* Meyer is a form with follicles of such a degree of rugosity that they appear squamate; *P. grandiflora* Hook. has larger flowers and lanceolate leaves rather more pubescent beneath than above. Except for the characters mentioned, these variants possess all of the attributes of *Sarcostemma Gilliesii*. Whether they are to be recognized as varieties is a matter of preference which should, however, be based upon experience with the genus as a whole. I prefer not to do so until population studies can be made. I can find no altitudinal, habitat, or flowering period differences among the various subgroups of *S. Gilliesii*, except for the obvious fact that those from the more southern stations experience greater aridity.

Sarcostemma Gilliesii is a sub-shrub of twining to trailing habit. Like other desert species of the genus, it makes tangled masses several feet in diameter, climbing over rocks and shrubs, as well as itself, in dry, rocky soil. Occasionally it may climb into trees. It grows at altitudes from 450 to 3000 feet and has been collected in flower from September to March. I have seen no fruit, except for a single distorted follicle collected in August. An interesting specimen was collected among ballast at Karghus Point, New Jersey. According to the collector, Dr. Henry Leffmann, in a letter to Asa Gray, it was a perennial which flowered abundantly but did not fruit.

BRAZIL (?): Río Negro, *D'Orbigny 246*, type of *S. incanum* Decne.

BOLIVIA. COCHABAMBA: quebradas de Totara, *Steinbach 5992*; near Yungas, *Rusby 1973*. LA PAZ: near Sorata, *Mandon 353*, type of *Amblystigma pedunculare* Benth. TARIJA: near Tarija, *Fiebrig 2668*.

ARGENTINA. BUENOS AIRES: Monte Hermoso, *Carette s. n.*; island near Buenos Aires, *Tweedie s. n.*; Isla Martín García, *Cabrera 2846*. CATAMARCA: Capitál, Alta Chaya, *Castillón 1071*; El Cajon, Las Visacheras, *Castillón 3349*; Pomán, near Pomán, *Castillón 1029* (part); Ambato, El Potrero, *Castillón 1069*; Capitál, *Castillón 1072, 1958*; Valle de Santa Maria, Punto de Balasto, *Schreiter s. n.*; Andalgalá, Andalgalá, *Jörgensen 1095*; Tinogasta, Vallecito a Agua Negro, *Schreiter 6284*; Ambato, El Rodeo, *Castillón s. n.* CHACO: Nueva Pompeya, *Jörgensen 3025*. CÓRDOBA: Córdoba, Río II, *Stuckert 23264*; Malagueño, *Bartlett 20069*; near La Falda, *Job 515*; *Kuntze s. n.*, *Stuckert s. n.*, *Lössen 39*. FORMOSA: Guayculec, *Jörgensen 3184*. JUJUY: Tilcara, Cerro Péna, *Venturi 4939*; Tilcara, Maimara, Hualchin, *Budin s. n.*; Humahuaca, quebrada de Humahuaca, El Volcán, *Castillón 6421*; Volcán, Loma de Laguna, *Schreiter 2590*; Tilcara, quebrada de Euasamayo, *E. K. Balls B5962*. LA RIOJA: Famatina, Famatina, *T. Meyer 4255*; Generál Lavalle, Guandacol, *T. Meyer 4182*. MENDOZA: Pampa de St. Rafael, *Wilczeb 281*; Maipu, Barrancas, *Bartlett 19335*; Potrerillos, *Bartlett 19325*; between Villavicencia and Uspullata, *Senn 4452*. RÍO NEGRO: vicinity of Generál Roca, *Fischer 110*. SALTA: San José, *Lorentz & Hieronymus 221*; Capitál, Salta, *Hunziker 2722*. SANTIAGO DEL ESTERO: Gramilla, *Venturi 10281*. TUCUMÁN: Trancas, Tapia, *Schreiter 3495*; Río Chico, La Cocha, *Bailetti 148, 350, 545*; Trancas, Raco, *Venturi 1202*; Trancas, Chaspiyacu, *Schreiter 5514*; Capitál, *Lillo 320, 11864*; Tafí, Amaicha, *Castillón 2485*, *Schreiter 5511*; Trancas, Tapia, *Venturi 1114*, *Lillo 4840*, *Rodriguez 596*; Trancas, Vipos, *Venturi 1717*, *Schreiter 4540*, type of *P. Schreiteri* Meyer; Burruyacu, Cerro del Campo, *Venturi 7720*; Capitál, Villa Luian, *Venturi 280*; Capitál, Barranca Colorada, *Venturi 4095*; Tafí, La Casita, region del Aliso, *Lillo 7350*; Burruyacu, Cerro de Durasnillo, *Monetti 1992*; Tucumán, *Tweedie s. n.*, type of *P. grandiflorum* Hook.

17. SARCOSTEMMA **Vaileae** (Rusby) R. Holm, comb. nov.

Oxystelma Vaileae Rusby, in Bull. N. Y. Bot. Gard. 4:315. 1907. (T.: *Bang 985 in Herb. N. Y. Bot. Gard.*!).
Philibertia albiflora Lillo, in Physis 4:428. 1919. (T.: *Castillón 9463 in Herb. Lillo!*).

Stems twining, minutely pilosulose in lines decurrent from the petioles; lateral branches many. Leaves deltoid-lanceolate, acute to obtuse, shallowly cordate, the lobes descending or diverging, 2.9–7.0 cm. long, 0.8–2.9 cm. wide, glabrate to minutely pilosulose above, glabrate to subtomentose beneath, with one or more glands on the midrib at the base; petiole 1.9–2.9 cm. long. Inflorescences racemiform, 2- to 7-flowered; peduncle 1–5 cm. long, minutely pilosulose; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–2.5 cm. long, minutely pilosulose. Calyx lobes narrowly lanceolate, 3 mm. long, pilosulose without, scatteringly pilosulose within; squamellae numerous, indefinitely distributed within the calyx. Corolla campanulate, yellowish green to cream-colored, the tube 6 mm. long, the lobes acute, 2.5–3.0 mm. long, pilosulose without, glabrous within. Gynostegium 3 mm. high, the column 0.75 mm. long. Anthers 1.5 mm. long, the apical appendage rhomboidal, the pollinium-sacs clavate-oblongoid, 0.5 mm. long, with sagittate corpusculum; ring of the corona nearly obsolete; vesicles of the corona obovoid-oblongoid, with a short apical appendage, rarely with a vertical ventral keel, constricted at their insertion upon the column, 1.5 mm. long. Ovaries 2 mm. long, glabrous; stigma-head cylindrical, shortly 2-fid. Follicles and seeds unknown.

Sarcostemma Vaileae is most closely related to *S. Gilliesii*. It may perhaps represent a race of that variable species which has become stabilized and no longer intergrades to an appreciable extent. Although the species are rather close morphologically, there is little difficulty in distinguishing them, for they differ not only in many vegetative characters but in several aspects of the flower as well. A general scarcity of pigmentation gives the stem, leaves, and flowers a characteristic pallid aspect. The column and anthers, on the other hand, are unusually dark, or even black, contrasting strongly with the white or yellow corona vesicles and corolla.

The collection, *Fiebrig 3084*, is the type of *Philibertia picta* Schltr. and is a form with dark flowers and light column. It is possibly a hybrid between *S. Vaileae* and *S. Gilliesii*, for the vegetative characters are those of the former species, but I prefer not to place the name in synonymy of either of these species at present. There are several collections, e. g. *Steinbach 8726*, which superficially match the type of *P. picta*, but which actually are easily referable to *S. solanoides* on the basis of the pubescence of the leaves, the character of the gynostegium, and the inflorescence.

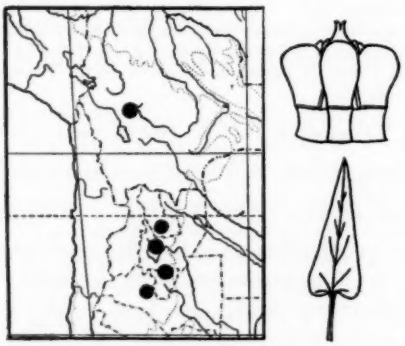

Fig. 20. Distribution, gynostegium, and leaf of *S. Vaileae*.

Sarcostemma Vaileae has been collected in Bolivia and northern Argentina in open woods at altitudes from 3500 feet to 6000 feet. Flowering specimens are dated December to March.

BOLIVIA. COCHABAMBA: Cochabamba, *Bang 985*, type of *Oxystelma Vaileae* Rusby. ARGENTINA. CATAMARCA: Andalgalá, El Candado, *Jörgensen 1239*; Belén, Villavil, *Schreiter 10255*. JUJUY: Tumbaya, El Volcán, *Castillón 6473*. SALTA: Rosario de Lerma, Campo Quijano, *Venturi 8064*; Cerro San Bernardo, *West 6130*. TUCUMÁN: Trancas, San Pedro de Colalao, *Castillón 6781*.

18. SARCOSTEMMA SOLANOIDES (HBK.) Decne. in DC. Prodr. 8:541. 1844.

Philibertia solanoides HBK. Nov. Gen. et Sp. Pl. 3:196, *t. 230*. 1819. (T.: *Humboldt & Bonpland s. n. in Herb. Paris*!).
Philibertia flava Meyen, Reise 1:466. 1834, ex char.
Pentagonium flavum (Meyen) Schauer in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.

Sarcostemma hastatum Decne. loc. cit. 1844. (T.: *Dombey s. n. in Herb. Paris!*).
Sarcostemma marsupiflorum Decne. loc. cit. 1844. (T.: *Cuming 983 in Herb. Kew.*!).
Sarcostemma quadriflorum Decne. loc. cit. 542. 1844. (T.: *Matthews 576 in Herb. Delessert*!).
Sarcostemma variifolium Decne. loc. cit. 1844. (T.: *Dombey s. n. in Herb. Paris*!).
Oxystelma solanoides (HBK.) K. Schum. in E. & P. Natür. Pflanzenfam. 4^2:229. 1895.
Philibertia Weberbaueri Schltr. in Engl. Bot. Jahrb. 37:607. 1906. (T.: *Weberbauer 2742 in Herb. Berol.*!).
Philibertia quadriflora (Decne.) Schltr. in Fedde's Repert. 13:282. 1915.
Philibertia variifolia (Decne.) Schltr. loc. cit. 283. 1915.
Philibertia obtusiuscula Malme, in Ark. Bot. $25A^7$:16, *fig. 2*. 1933. (T.: *Hicken 39 in Herb. Stockholm*!).
Philibertia obtusata Malme, op. cit. $26A^4$:41. 1934, *sphalm.*

Stems twining or trailing, minutely puberulent; lateral branches many. Leaves ovate to deltoid-lanceolate, acute to acuminate, deeply cordate, the lobes diverging, 2.0–3.5 cm. long, 0.9–1.4 cm. wide, membranaceous to subcoriaceous, often somewhat undulate, scatteringly puberulent above, subtomentose beneath, with one or more glands on the midrib at the base; petiole 0.6–0.9 cm. long. Inflorescences umbelliform, 4- to 10-flowered; peduncle stout, slightly recurved at the apex, 3.5–7.5 cm. long, minutely puberulent; bracts linear, 0.1–0.2 cm. long; pedicels 0.9–1.3 cm. long, minutely puberulent. Calyx lobes narrowly lanceolate, 3–5 mm. long, scatteringly to densely puberulent without, glabrous within; squamellae absent, single, or paired. Corolla rotate-subcampanulate, greenish-yellow to cream with red or purple spots within, or uniformly greenish-yellow, the tube 5–6 mm. long, the lobes acute, 3–4 mm. long, puberulent without, glabrous within. Gynostegium 2–3 mm. high, vernicose, the column about 1 mm. long. Anthers 1.0–1.5 mm. long, the apical appendage deltoid, the pollinium-sacs compressed, obclavate, 0.5 mm. long, with sagittate corpusculum; ring of the corona short; vesicles of the corona truncate-oblongoid, with or without a small apiculation at the apex, 1.5 mm. long. Ovaries 2 mm. long, glabrous; stigma-head cylindrical, obscurely depressed or 2-lobed apically. Follicles ovoid, minutely puberulent, finely striate, 4.4 cm. long, 0.8 cm. thick; seeds unknown.

The umbelliform inflorescence and rotate-subcampanulate flowers at once distinguish this species from others of the subg. OXYSTELMA. Superficially, in fact, S. *solanoides* appears to pertain rather to the subg. CERAMANTHUS. This resemblance is most probably due to convergence, however, for not only the structure of the gynostegium, but also the detailed morphology of the inflorescences and vegetative organs relates it clearly to OXYSTELMA. The corona ring is very abbreviated and free from the corolla only at the outermost part, and the gynostegium is vernicose. The inflorescence, while umbelliform, is slightly recurved at the apex, a condition which does not obtain in subg. CERAMANTHUS.

Sarcostemma solanoides apparently is a trailing plant forming dense mats (but not rooting at the nodes), in dry, rocky, or gravelly soil or on talus slopes. In more favorable habitats it climbs into shrubs. It is reported that the herbage has an onion-like odor when crushed, presumably like that of S. *hirtellum*. The species

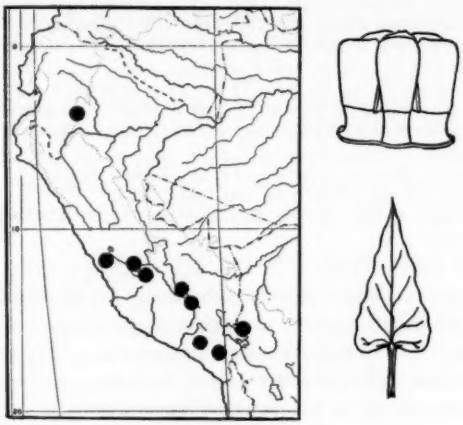

Fig. 21. Distribution, gynostegium, and leaf of S. *solanoides*.

ranges from southern Ecuador to northern Bolivia and has been collected in flower from February to April at altitudes from 6500 to 15000 feet.

ECUADOR. LOJA: between San Pedro & Chinchas, ca. 55 km. from Loja, *Espinosa 1291*; Hac. Huaico-Pamba, ca. 55 km. S Loja, *Espinosa 2303*.

PERU. AREQUIPA: Arequipa, *Pennell 13195*. CUZCO: Paruro, Huanoquite, *Vargas 2347*; Cuzco, Callchaca, *Vargas 5507*; Canchis, slopes of Sicuani, *Vargas 9829*, *Stafford 359*; Sicuano, *Hicken 39*, type of *P. obtusiuscula* Malme. LIMA: Huarochiri, valley of Río Rimac, 81 km. E of Lima, *Goodspeed & Metcalf 30229*; Huarochiri Matucana, *Weberbauer 5257*, *Macbride 2889*, *Macbride & Featherstone 208*; Orroya near Lima, *Kalenborn 30*. HUANCAVELICA: Angaraes, 3 km. W of Huanta, *Stork & Horton 10809*; Tayacaja, Montaro Valley near La Mjorada, *Weberbauer 7610*; Tayacaja, Montaro Valley below Colabamba, *Weberbauer 6453*. LIMA: Río Blanco, *Macbride 3042*. MOQUEGUA: Carumas, *Weberbauer 7298*.

BOLIVIA. COCHABAMBA: Toluon Sacaba, *Steinbach 8426*. LA PAZ: near Sorata, *Mandon 360*.

19. SARCOSTEMMA **stipitatum** (Lillo) R. Holm, comb. nov.

BOLIVIA. COCHABAMBA: Toulon Sacaba, *Steinbach 8726*. LA PAZ: near Sorata,

Stems twining, glabrous or minutely pilosulose in lines decurrent from the petioles; lateral branches relatively few. Leaves lanceolate, acuminate, cordate, the lobes descending, 5.5–7.5 cm. long, 1.5–3.0 cm. wide, firmly membranaceous, undulate-crispate, essentially glabrous on both surfaces, the veins pilosulose, with one or more glands on the midrib at the base; petiole 1.0–2.5 cm. long. Inflorescences racemiform, 4- to 8-flowered; peduncle 3.0–5.8 cm. long, minutely appressed-pilosulose; bracts linear, 0.2–0.3 cm. long; pedicels 0.7–1.1 cm. long, minutely pilosulose. Calyx lobes narrowly lanceolate, 3.5 mm. long, appressed-pilosulose on both surfaces; squamellae few or absent, alternate. Corolla urceolate-campanulate, the tube 6 mm. long, the lobes bright brown, obtuse, 3 mm. long,

puberulent without, glabrous within. Gynostegium 3.5 mm. high, the column 1.5 mm. long. Anthers 1.5 mm. long, the apical appendage ovoid, slightly emarginate, the pollinium-sacs clavate-oblongoid, somewhat flattened, with a sterile hyaline region at the attachment of the translator arm, 0.75 mm. long, with narrowly ellipsoid corpusculum; ring of the corona nearly obsolete; vesicles of the corona oblate-spheroid, 1 mm. long. Ovaries 2 mm. long, glabrous, the styles well-marked; stigma-head cylindrical, obscurely depressed apically. Follicles and seeds unknown.

Sarcostemma stipitatum surely is the most distinctive species of the subg. OXYSTELMA, with its urceolate corolla, greatly reduced corona vesicles, and pollinia with a sterile, hyaline region, yet, surprisingly enough, it has never been referred to another genus. It is without obvious relationship to any other species to my knowledge. Rather sharply localized in northern Argentina, it grows at altitudes from 4500 to 5500 feet, and flowers from November to January.

ARGENTINA. SALTA: La Candelaria, Cuesta del Unquillo, *Schreiter 9372*. TUCUMÁN: Tafí, La Hoyada, *Venturi 1536;* Quebrada del Durasnillo, *Lillo 2621, Schreiter 8703;* Tafí, Cumbre del Siambón, *Venturi 2821*.

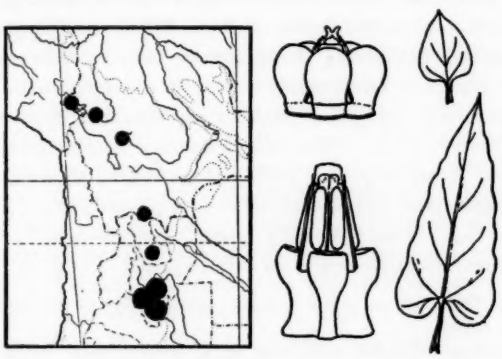

Fig. 22. Distribution of S. *stipitatum* (small dots), of S. *lysimachioides* (large dots). Gynostegium and leaf of S. *lysimachioides* (upper figures), of S. *stipitatum* (lower figures).

20. SARCOSTEMMA **lysimachioides** (Wedd.) R. Holm, comb. nov.

Lugonia lysimachioides Wedd. Chlor. And. 2:49, *t. 54.* 1857. (T.: *Weddell 4136 in Herb. Paris*!).
Philibertia lysimachioides (Wedd.) T. Meyer in Descole, Gen. et Sp. Pl. Arg. 2:177. 1944.

Stems prostrate, trailing from a short woody caudex, more or less articulate, minutely appressed-pilosulose; lateral branches many on the old stems. Leaves ovate, acute to obtuse, usually cordate, sometimes truncate or obtuse, 0.4–1.0 cm. long, 0.3–0.6 cm. wide, subcoriaceous, revolute, essentially glabrous on both sur-

faces, the midrib puberulous, usually without glands at the base (rarely a very few); petiole 0.2–0.4 cm. long. Inflorescences racemiform, 1- to 3-flowered; peduncle 0.4–0.7 cm. long, minutely pilosulose; bracts linear, 0.1–0.2 cm. long; pedicels 0.3–1.0 cm. long, appressed-pilosulose. Calyx lobes lanceolate to oblanceolate, 4 mm. long, puberulent without, glabrous within; squamellae alternate, 3–5, upon a thickened pad. Corolla campanulate, the tube 5.5 mm. long, the lobes deep orange to red, ovate, broadly obtuse, 5.5–6.0 mm. long, scatteringly puberulent without, glabrous within. Gynostegium 3 mm. high, the column 0.5 mm. long. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs clavate, 0.5 mm. long, with sagittate corpusculum; ring of the corona obsolete; vesicles of the corona ovoid, slightly constricted at their insertion upon the column, 1 mm. long. Ovaries 2 mm. long, glabrous, the styles well-marked; stigma-head conical, 2-apiculate, the apiculae flattened. Follicles fusiform, 1.9 cm. long, 0.3 cm. thick, minutely puberulent, finely striate; seeds unequally biconvex, 3 mm. long, 1.5 mm. wide, rugose on both surfaces, the margin entire; coma about 0.8 cm. long.

A plant of pronounced alpine modification, S. *lysimachioides* grows at heights of 9000 to 14000 feet in the Andes of Peru, Bolivia, and Argentina. It is a prostrate, perennial herb forming clumps among bunch grasses and shrubs. To precisely which species of *Sarcostemma* it is most closely related I am unable to determine. The corolla and gynostegium are reminiscent of S. *solanoides*, but the fact that the corolla is adnate to the column forms a clear distinction. This condition otherwise is found only in S. *andinum*, yet despite the fact that the latter and S. *lysimachioides* were included in the same segregate genus *(Lugonia)* in the past, I feel that they are only distantly related. *Sarcostemma lysimachioides* has been found in flower from November to February, and in fruit in April.

PERU. PUNO: Baja Isla del Lago Titicaca, *Mexia 7789;* Granja Salcedo, Cañon of Viscachani, *Mexia 04261.*

BOLIVIA. AYOPAYA: *Weddell 4136,* type of *L. lysimachioides* Wedd. CHUQUISACA: Tomina, *Weddell s. n., 3885;* Cinti, *Weddell 3938.* COCHABAMBA: Cochabamba, *Weddell 4102;* Ansaldo, *Cárdenas 2292.* LA PAZ: La Paz, *Buchtien 67;* Omasuyos, *Mandon 359.* TARIJA: about 45 km. NE of Villazón on Villa Montes, *West 8234;* Escayache bei Tarija, *Fiebrig 3033.*

ARGENTINA. JUJUY: Tumbaya, Mula Muerta, *Castillón 6665.*

Section 2. PENTACYPHUS (Schltr.) R. Holm, stat. nov.

Pentacyphus Schltr. in Engl. Bot. Jahrb. 37:605, *fig. 3.* 1906, as genus.

This section includes two species in which the corolla tube is adnate to the column and pubescent within, forming five hairy pouches alternating with the stamens. The column has deep grooves, and the large flowers have broadly obtuse corolla lobes.

KEY TO THE SPECIES

a. Leaves oblong-lanceolate, cordate; inflorescences racemiform, 2-flowered; corona segments undivided, depressed dorsally ..... 21. *S. andinum*
aa. Leaves obovate-elliptic, cuneate; inflorescences umbelliform, several-flowered; corona segments bipartite ..... 22. *S. Lehmannii*

21. SARCOSTEMMA **andinum** (Ball) R. Holm, comb. nov.

Lugonia andina Ball, in Jour. Linn. Soc. Lond. 22:49. 1887. (T.: *Ball s. n. in Herb. Kew.*!).

Pentacyphus boliviensis Schltr. in Engl. Bot. Jahrb. 37:605, *fig. 3*. 1906, ex char. (T.: *Weberbauer 179 in Herb. Berol.*).

Stems twining, glabrous or pilosulose in lines decurrent from the petioles; lateral branches many. Leaves oblong-lanceolate, acute to mucronate, cordate, the lobes descending, 1.5–5.0 cm. long, 0.6–2.4 cm. wide, membranaceous, glabrous above, the veins pilosulose, with one or more glands on the midrib at the base, appressed-pilosulose beneath; petiole 0.6–2.5 cm. long. Inflorescences racemiform, consisting of two 1-flowered cymules; peduncle 1–2 cm. long, minutely pilosulose; bracts linear, minute; pedicels 0.5–1.5 cm. long, minutely puberulent. Calyx lobes narrowly lanceolate, 8 mm. long, sparsely puberulent without, glabrous within, ciliolate; squamellae absent. Corolla campanulate, green to yellow, the lobes with a purple to dark red spot at the base, the tube 9.5 mm. long, glabrous without, pilosulose within, adnate to the column directly below the anthers forming five hairy pouches, each with a tuft of longer hairs borne upon a thickened pad at the base, the lobes broadly ovate, obtuse, 9 mm. long, glabrous on both surfaces. Gynostegium 7 mm. high, the column 4 mm. long, grooved between the stamens with the margins of the groove produced and arrect. Anthers 1.5 mm. long, the apical appendage oblong, mucronate, the pollinium-sacs oblongoid, somewhat flattened, 0.75 mm. long, with ellipsoid-sagittate corpusculum; ring of the corona obsolete; vesicles of the corona obovoid, depressed dorsally toward the apex, attenuate, 3 mm. long. Ovaries 4 mm. long, glabrous, the styles not well-marked; stigma-head 2-lobed. Follicles and seeds unknown.

Sarcostemma andinum has diverged markedly in a number of ways from the general OXYSTELMA type. The corolla is adnate to the column along five lines directly below the anthers; below the point of attachment the corolla tube is pilosulose within, so that five hairy pouches are formed. Exterior to these, the corolla is quite glabrous. The highly vernicose gynostegium is similarly extreme: as in several species of the subg. CERAMANTHUS, the column is grooved or invaginated directly below the anther wings, but in this case, the margins of the groove are produced at an angle of about 45° to the column. Continuous with the anther wings they, in effect, extend the latter the length of the column, down into the pouches, to the base of the corolla. Such modifications surely must adapt the flower very specifically to its insect pollinator.

These distinctive features of the plant, together with others of the inflorescence and pollinia, preclude relating S. *andinum* to any other species in the family except S. *Lehmannii*. The latter species is so distinct that it also has been considered, with

a certain justification, as a representative of a monotypic genus. I see no advantage in maintaining monotypic genera for such plants, however. To include them within another genus, separating them from the other species with appropriate subgeneric categories, at least indicates their affinities in a general way. Isolating them in a family with no adequate system of tribes conveys nothing as to their relationships, morphological or otherwise, and makes identification immeasurably more difficult.

Sarcostemma andinum is a widespreading vine, which grows in shady or open situations, climbing over shrubs and trees. It has been collected at altitudes from 5500 to 13000 feet; flowering specimens are dated from February to June.

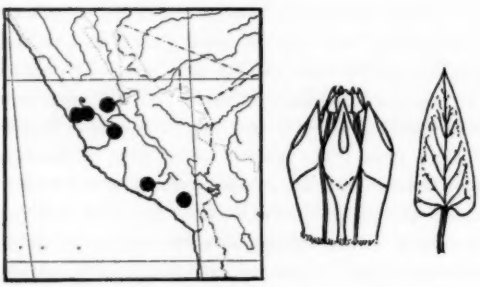

Fig. 23. Distribution, gynostegium, and leaf of *S. andinum*.

PERU. AREQUIPA: *Weberbauer 6860*. HUANCAVELICA: Castrovirreina, near Córdoba, *Metcalf 30274*. LIMA: Huarochiri, valley of Río Rimac, 50 km. E of Lima, *Goodspeed 33090*; Huarochiri, Infiernillo, *Goodspeed, Stork & Horton 11602*; Huaros, *Pennell 14722*; Río Blanco, *Killip & Smith 21701*, *Macbride & Featherstone 725*; Matucana, *Macbride 2951*; near Lima, *Kalenborn 30*; Chicla, *J. Ball s. n.*, type of *L. andina* Ball. MOQUEGUA: Carumas, *Weberbauer 7258*.

22. SARCOSTEMMA **Lehmannii** (Schltr.) R. Holm, comb. nov.

Tetraphysa Lehmannii Schltr. in Engl. Bot. Jahrb. 37:616. 1906, ex char. (T.: *Lehmann 8516 in Herb. Berol.*).

Stems twining, more or less articulate, glabrous; lateral branches few. Leaves obovate-elliptic, acute, cuneate, 9.5 cm. long, 4.0 cm. wide, coriaceous, glabrate, with several glands on the midrib at the base; petiole 1.5 cm. long. Inflorescences umbelliform, several-flowered; peduncle 2 cm. long, glabrous; bracts linear-lanceolate, 0.3–0.4 cm. long; pedicels 2.5 cm. long, glabrous. Calyx lobes obovate-elliptic, 7 mm. long, glabrous on both surfaces; squamellae alternate, solitary. Corolla campanulate, cream with reddish-purple spots within, the tube 7 mm. long, glabrous without, pilosulose within, adnate to the column directly below the anthers forming five hairy pouches, the lobes broadly ovate, obtuse, 15 mm. long, glabrous without, glabrous to minutely pilosulose within. Gynostegium 7 mm. high, the column 4 mm. long, grooved between the stamens (with the margins of

the groove slightly produced) and directly below the corona vesicles. Anthers 1.5 mm. long, the apical appendage oblong, the pollinium-sacs oblongoid, somewhat flattened, 0.5 mm. long, with ellipsoid corpusculum; ring of the corona obsolete; vesicles of the corona bipartite, consisting of two somewhat flattened, ovate, attenuate segments, joined toward the apex, exceeding the stigma-head in length. Ovaries 3 mm. long, glabrous, the styles not well-marked; stigma-head 2-lobed. Follicles and seeds unknown.

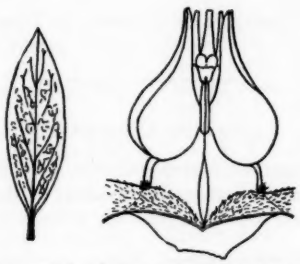

Fig. 24. Leaf and gynostegium of *S. Lehmannii.*

A most rare and distinctive species. I have not seen the type, but the description and figures of Schlechter leave no doubt as to its identity with the single subsequent collection available to me. The gynostegium is highly vernicose and superficially similar to that of *Sarcostemma andinum.* In addition to the five grooves in the column which lead into the pouches of the corolla tube, there are five longitudinal clefts which divide the corona vesicles, and the column directly below them, to the corolla. As I have indicated in the discussion of the preceding species, *S. Lehmannii* is probably most closely related to *S. andinum.* The evolution of the gynostegium may be pictured as involving an extension of the dorsal depression of the corona vesicles of the latter species, until it extends to the corolla. The advantages of such an arrangement to the plant are not in the least apparent, however. If these forms are to be related to any group in the Asclepiadaceae, it must surely be to *Sarcostemma.* I have merged them with that genus, indicating their divergence by sectional segregation, rather than let them drift among the many other monotypic genera without obvious mooring.

Sarcostemma Lehmannii has been collected in dense woods at altitudes of about 8000 feet, and was in flower in May and October.

COLOMBIA. CAUCA: vicinity of Popayan, *Lehmann 8516,* type of *T. Lehmannii* Schltr., not seen.

ECUADOR. LOJA: between Tambo Cachiyacu, La Entrada, and Nudo de Sabanillas, *Steyermark 54471.*

IMPERFECTLY KNOWN SPECIES

Sarcostemma Jacquini Decne. in DC. Prodr. 8:542. 1844. Description inadequate, no type cited.

Sarcostemma trichopetalum Alv. Silv., Fl. Serr. Mineir. 18. 1908. Publication unavailable to me.

EXCLUDED SPECIES

Philibertia anomala T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:277. 1912. = BLEPHARODON MUCRONATUM (Schlecht.) Decne.

Lugonia micrantha Malme, in Nova Acta Acad. Soc. Upsal. IV, 1^1:115. 1905. = APHANOSTELMA MICRANTHUM (Malme) T. Meyer.

Philibertia ? scandens Gomez, in Anal. Hist. Nat. Madrid 23:276. 1894. = FISCHERIA SCANDENS DC.

Philibertia viridiflora (Torr.) Britt. & Rusby, in Trans. N. Y. Acad. Sci. 7:11. 1887, sphalm.

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Italicized numbers refer to the collectors' numbers, *s. n. (sine numero)* to unnumbered collections; parenthetical numerals indicate the numbers of the taxonomic entities recognized in this monograph. Only specimens from the Western Hemisphere are included.

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THE GRAIN AMARANTHS: A SURVEY OF THEIR HISTORY AND CLASSIFICATION*

JONATHAN DEININGER SAUER**

Since man first began digging, clearing, and burning the natural vegetative mantle of the earth, certain plant groups have multiplied and spread as others declined and retreated; they have thrived in the midst of the general destruction as weedy followers or cultivated allies of civilization. In the great story of how such plants and human civilizations have consorted, migrated, and evolved together on the earth, the amaranths have played a part which is of uncommon ethnological and botanical interest.

For the ethnologist, the amaranths present problems of curiously widespread and ancient culture traits. The plants are firmly entrenched in the religious and economic lives of various Old and New World peoples as wild or cultivated grains, pot-herbs, dye-plants, fetishes, and ornamentals. Insight into their culture history should help in understanding the larger problem of the origin and diffusion of cultivated plants.

For the botanist, the amaranths present a problem of strikingly contrasting responses to man by different members of a single genus. Some species have remained aloof as unobtrusive wild endemics. Others have moved uninvited into clearings and fields; with the unintentional help of man they have become aggressive and widespread weeds. Still others have entered cultivation and become deliberately propagated wards of man. Insight into the unlike behavior of these different amaranths should help in understanding the larger problem of changes in character and distribution patterns of plants since the coming of man.

In spite of its uncommon interest, the story of the amaranths has remained neglected and obscure. Perhaps this is partly because the problem cannot be readily attacked either by a strictly ethnological or by a strictly taxonomic approach. The ethnologist is confronted by near chaos in the classification and nomenclature of this group; he can make little headway until there is clearer definition of the botanical entities which have entered into culture history. The taxonomist is confronted by a dim and fragmentary picture of the relationships of man to this group; he can make little headway until there is clearer recognition of the effects of artificial processes in the evolution and distribution of the botanical entities. A combined ethnological and botanical investigation would seem to be the only way to escape from the dilemma.

In this paper these two complementary lines of approach will be tried on a limited sector of the general problem. The full story of all the wild, weed, and cultivated species of this genus is much too massive a problem to be attacked here. This paper will focus on the cultivated grain amaranths; even within this restricted

* An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Washington University.

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group, it can make no more than a beginning.

The grain amaranths are an attractive starting point for several reasons. Of all the amaranths, the grain species seem to have been most closely and most anciently allied with man; they have left the deepest imprint on human cultures and received in return the clearest marks of human selection and dispersal. A fund of basic information on them has long been accumulating, both as historical records and as herbarium collections. The few existing general statements of the story have exploited only a small part of this fund and have made no attempt to combine botanical and ethnological evidence.

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I. HISTORY OF CULTIVATION AND USE

The imperfectly known culture history of the grain amaranths will be followed in geographic sequence through four continents. The trail begins very faintly among the Indians of the southwestern United States, becomes gradually more distinct through northwestern Mexico as the great central Mexican stronghold of the crop is approached, and gradually fades again in southern Mexico. A small isolated center is found in Guatemala, and a larger one in the Andes extending from Peru through Bolivia into northwestern Argentina. On the other side of the Pacific an indistinct trail runs from Manchuria through interior China to a major center in the Himalayas and disappears gradually into Afghanistan and

Persia. There is a small outpost in southern India and Ceylon. Finally, there are vague traces of the crop in Africa.

UNITED STATES

The role of grain amaranths among the Indians of the United States is an unsolved puzzle. The enormous literature on aboriginal cultures contains only a few hints and fragments of information suggesting cultivation of the plants.

Caches of seeds identified as amaranths have turned up in various archaeologic sites, such as Snaketown in Arizona (Castetter and Bell, 1942, p. 35) and the Bluff-Dwellings of the Ozarks (Gilmore, 1931, p. 97). The Ozark material was identified for Gilmore by Safford, who ventured no guess as to whether the amaranth seeds were from cultivated plants (Jones, letter[1]). In his published report on this material, Gilmore surmised that the plants were cultivated, but in 1936 in a letter to Edgar Anderson he wrote that this was doubtful. It is well known that, in recent times and presumably in the past, a great many American Indian tribes gathered wild amaranth seeds along with almost everything else fit to eat in their regions. Unfortunately, the seeds of cultivated and wild amaranths are often indistinguishable, so that the prehistoric seed caches are inconclusive as evidence on the question of cultivation. Volney Jones informs me that all of the archaeologic seed finds he has seen, including the Snaketown material, are so small that they probably represent wild plants.

There are some puzzling historical records which report grain amaranths in the Southwest. In 1875 a new species, *Amaranthus leucocarpus*, was described on the basis of plants grown at Harvard from a mixture of various seeds collected in Arizona by J. W. Powell (Watson, 1875, p. 347). The only information accompanying the description was that the seeds were used by the Arizona Indians for food. The seeds are light-colored and therefore almost certainly from a cultivated plant; I know of no example of a wild or weed amaranth with pale seeds. Although Powell had traveled widely in the Southwest prior to 1875 he worked mostly in northern Arizona, so it seems likely that he collected the seeds there. They may have been grown by the Paiutes. Edward Palmer, a contemporary of Powell, wrote (1878, p. 603) that the Paiutes regularly cultivated two species of amaranth, one of which was *A. leucocarpus;* they called the plants *camoot*, and made a bread or mush from the meal. Some later writers made cryptic statements that the Arizona Indians cultivated amaranths for seed (Watson, 1880, p. 41; Uline and Bray, 1894, p. 314), but gave no details.

Various of the southwestern Pueblo peoples still cultivate amaranths as dye plants but make no use of the seeds (J. D. Sauer, in press). Ethnically and botanically, this crop seems to be distinct from *A. leucocarpus* and will not be discussed here.

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[1]Complete names and addresses of persons providing unpublished data are cited in the List of Sources at the end of the paper.

MEXICO

Hernán Cortés, writing the second letter to his king on the conquest of Mexico, recorded what may have been the first European contact with grain amaranths. He wrote that the heathen idols of the Aztecs were made of a dough of various seeds, milled and kneaded with the blood of human sacrifices (1520, p. 33). Cortés attempted no identification of the seeds included in the recipe, but there is reason to believe that grain amaranths were an essential ingredient.

It has been known for a long time that the ancient Mexicans made idols of a dough called *zoale* and that this dough was made from the seeds of an important crop plant called *huauhtli* by the Indians and *bledo* by the Spanish colonists. The botanical identity of this crop remained a mystery until the 20th century. Gallatin (1845, p. 117) mentioned the crop but was unable to imagine what it might have been. He wrote: "I cannot discover what is meant by *guatli*. It is interpreted as being *semilla de bledo*, but I am not aware of any other native grain than maize having been an article of food of such general use, as the quantity mentioned seems to indicate." Payne (1892, 1:354) believed *huauhtli* was a cereal grass and called it "wheat of Michoacan." Bourke (1892, p. 522) came to the bizarre conclusion that *huauhtli* must have meant tule pollen. Finally, Urbina (1903, p. 589) and Safford (1917, p. 290) decided that *huauhtli* was a grain amaranth and most later investigators have agreed with them (Bukasov, 1930, p. 504; Matschat, 1935, p. 26; Martínez, 1936, p. 24; Carl Sauer, 1936, p. 290; Caso, 1937, p. 46; Nuttall, 1937, p. 19; notations by Nicolas León in 1938 edition of Sahagún, 3:338, 364; Anderson and Barlow, 1943, p. 416; Hendrichs, 1945, 1:236).

PROBLEM OF BOTANICAL IDENTITY OF HUAUHTLI.—

A few recent workers have dissented from the majority interpretation and have suggested that *huauhtli* was a grain chenopod (Emmart, 1940, p. 321; Hunziker, 1943b, p. 319; Reed, 1944, p. 211). This possibility requires serious consideration. At the present time, the Mexicans cultivate some chenopods which look so much like grain amaranths that the two are often confused by casual observers. Modern records of the two crops can usually be clearly separated on the basis of recent herbarium specimens, photographs, and trustworthy field observations. However, the story of these plants cannot be traced very far without leaving the firm ground of certain identification.

Many of the relevant modern records and practically all of the older accounts were written by persons who knew little botany and used popular rather than scientific names. Only one of the early accounts (Hernández, ca. 1575c—see Appendix—D) gave Latin generic names for *huauhtli;* unfortunately, it was written before the time when such names had a consistent and definite meaning and in different passages *huauhtli* was identified as both *Atriplex* and *Blitum*, names which suggest both chenopods and amaranths.

The occasional plant descriptions in the old accounts are almost useless in identification; some mentioned plant color, but both amaranths and chenopods

may be green or reddish. The few references to seed color give a better clue. Some of the chenopods and amaranths grown in Mexico today have dull whitish seeds, but many of the chenopods have dull reddish seeds and many of the amaranths have shiny black seeds. I know of no cultivated red-seeded amaranths or black-seeded chenopods in Mexico. Sahagún (ca. 1570b—see Appendix—C) reported ceremonial use of whitish, red, and black *zoale* or paste of *bledo* seed. Pomar's report (1582—see Appendix—F) of two kinds of *huauhtli* seed, one like a flattened turnip seed and the other smaller and white, also suggests that both chenopods and amaranths were involved.

The best clues in the early literature to the identity of *huauhtli* are the crude drawings in two 16th century writings (Sahagún, ca. 1570a; Hernández, ca. 1575b). Sahagún's drawings show definitely that he applied the name *huauhtli* or *'vauhtli'* to more than one kind of plant. Some with dentate leaves (pl. 10 A-B) appear to be chenopods; others with entire leaves (pl. 10 C-D) look much more like amaranths. Hernández used a single illustration, apparently of a chenopod, but his text explains that he considered *huauhtli* a general term for a group of different plants, some used for grain, some for green vegetables, and some just weeds (see Appendix—D).

The Indians themselves probably used the name *huauhtli* for a variety of plants, grown for different purposes. Some of the compound names may well have been restricted to particular species. *Xochihuauhtli* (flower *huauhtli*) may have meant a chenopod whose inflorescences were cooked in the bud stage as a green vegetable as is commonly done in modern Mexico. *Nexhuauhtli* (ash *huauhtli*), like the common Spanish word for chenopods, *cenizo*, probably referred to the whitish appearance of some chenopods. *Tlapalhuauhtli* (red *huauhtli*) might have meant either a red-seeded chenopod or a red-leaved amaranth; similar names are used ambiguously for both plant and seed color by Mexicans at present. *Michihuauhtli* (fish *huauhtli*) and *tezcahuauhtli* (mirror *huauhtli*) probably referred to light- and dark-seeded amaranths, respectively, the former with pale seeds like little fish eggs, the latter with shiny black seeds.

Information on these specific plants would be required to determine which were grown as grain crops. Unfortunately, the early accounts ordinarily used the simple name *huauhtli* with no prefix. Only *michihuauhtli*, which seems to have been an amaranth (pl. 10 C), was definitely regarded as a grain crop (Hernández, ca. 1575c—see Appendix—D; Pomar, 1582—see Appendix—F). Hernández has a rather ambiguous statement which implies that the seeds of *tlapalhuauhtli* and *nexhuauhtli* were also used.

There is another approach to this question, beyond the direct but hardly satisfactory internal evidence of the historical records; that is by comparison of the grain *huauhtli* picture with the distribution, uses and popular names of chenopods and amaranths grown in Mexico today.

The chenopod enthusiasts rest their case primarily on the cultivated species, *Chenopodium Nuttalliae* and *C. pueblense*, which they regard as surviving relics of

the once great grain crop (Emmart, 1940, p. 321; Hunziker, 1943b, pp. 319–322; Reed, 1944, p. 211, 1950, p. 139). It is assumed that a modern name, *huauhzontli*, sometimes reported for these plants, is derived from *huauhtli* (Robelo, 1904, p. 577). Actually *huauhzontli* may be a corruption of an entirely different word, *cuauhzontli*, which can be found in various early and recent writings and which I have often heard given to cultivated chenopods in modern Mexico.

In any case, the great weakness of the argument for chenopods as the major component of the ancient *huauhtli* crop is the poor correspondence between their present distribution and uses and the historical record of grain *huauhtli*. The ranges of the two overlap, but the coincidence is scarcely impressive. Cultivated chenopods have been found in the Federal District, the states of México, Guanajuato, Michoacán, Puebla, Oaxaca, Vera Cruz, and Tamaulipas (Safford, 1918, p. 524; Reed, 1944, p. 211; collections by Kelly, Carl Sauer and myself). This range excludes various states where *huauhtli* was an important crop and includes three states where the ancient grain crop was never reported.

The known uses of *cuauhzontli* bear little resemblance to the ancient uses of grain *huauhtli*. We shall see that *huauhtli* grain was commonly prepared for use simply by toasting. Powdered and stirred into water, the seeds made a drink which was considered delicious even by the early Spaniards. Mexican grain amaranths are quite palatable when toasted, but all the *cuauhzontli* seeds I have sampled have an extremely nasty bitter taste, which is not improved by toasting. They probably contain the same bitter substance present in the Andean *Chenopodium quinoa*. *Quinoa* grain is considered inedible when raw and is prepared for use by long boiling in many changes of water (Cook, 1904, p. 492). Chenopods are ordinarily cultivated in Mexico today not as grain crops but as green vegetables. The original account of the species *C. Nuttalliae* (Safford, 1918) reported that the immature tops of the plant were cut when in bud, dipped in batter, and fried. The only cultivated chenopods cited by Reed (1944, p. 211; 1950, p. 141) were used in exactly the same way. These plants have been collected by Isabel Kelly, Carl Sauer, and myself at seven other places in Mexico and in all cases the use was identical.

There is one Mexican state in which the seeds of *cuauhzontli* are known to be used as food. Hernández X. wrote me that in Michoacán the seeds of *C. Nuttalliae* are sometimes milled for tamales, although the plant is normally grown as a green vegetable. West (1948, p. 42) reported that white, black, and red-seeded amaranths are used as grain in Michoacán; all three are planted and harvested together and the seeds separated according to color only after threshing. Both the black and red seeds are usually milled for tamales. West has permitted me to grow his seed collections; of these the black and white seeds were all amaranths but the single collection of red seeds turned out to be a chenopod. West worked in this area in the dry season before planting time and had no chance to observe the plants, but he believes that all the red-seeded "amaranths" may turn out to be chenopods. Outside of Michoacán, grain chenopods seem to be unknown in Mexico today.

In contrast, the present range and uses of grain amaranths are strikingly like those of grain *huauhtli*, and the case for amaranths is strengthened by the records of popular names. It seems significant that the early writers consistently identified grain *huauhtli* as *bledo*, the ordinary Spanish name for amaranths, rather than as *cenizo*, the ordinary name for chenopods. For example, Sahagún (ca. 1570b, see Appendix—C) wrote that *huauhtli* was *bledo*, but that it was similar to *cenizo*. He identified only *huauhtli polocayo*, whose seeds were used as a starvation food, as *cenizo*. Slight variants of the words *huauhtli* and *zoale* have persisted in a few parts of Mexico as names for grain amaranths. In most of the country the name *huauhtli* has been gradually replaced by synonyms and is no longer applied to any plant.[2] The various synonyms can be traced down through the historical records as a continuous chain and finally tied to the present-day names of grain amaranths.

The details of the story appear in the following historical review. The individual pieces of evidence are often ambiguous and fragmentary, but they combine to give a strong impression that most of the writers were recording a single great grain crop, strikingly uniform in names and uses throughout its wide range. In some areas, we can be reasonably certain that this crop was a grain amaranth, pure and simple. In other areas, it may have been a complex of amaranths and chenopods, mixed in names, cultivation, and use as they seem to be in Michoacán at present. If so, the two plants have probably been so confounded that their stories may never be disentangled, and we can only hope that the confusion is confined to a fraction of the records. It seems almost inconceivable that plants which have left so faint a trace as the grain chenopods were more than a local and minor component of the great *huauhtli* crop.

HISTORY OF CEREMONIAL USE.—

Pre-Conquest.—The strange idols, great temples, and barbaric rituals of the pre-Conquest Mexicans fascinated many of the early chroniclers, particularly the priests. They gathered a wonderful amount of detailed information on heathen ceremonies and wrote long descriptions which contain much information on ceremonial plants.

One of the oldest and most copied documents on Aztec ritual is the so-called 'Ramírez Codex,' which describes the May festival honoring the war god, Huitzilopochtli (Anonymous, ca. 1550, pp. 128–135). The festival was observed throughout the empire, but the chief ceremony was at the temple pyramid in Tenochtitlán, the capital. The whole city attended, all the state and temple officials dressed in ceremonial garlands, feathers, and colored robes, according to rank. The intricate ritual involved dances, processions, singing, much noise of flutes, shell-trumpets, and drums, and human sacrifices in greater number than on any

[2] *Huauhtli* means nothing but fish eggs or insect eggs to most Mexicans at present. This two-fold meaning, apparently based on the roe-like appearance of chenopod and amaranth seeds, can be found in the earliest chronicles.

other day. The focus of all the activity was a huge idol of the god made of dough, as large as the regular idol of wood. The temple maidens, two days before the festival, had "milled a quantity of seed of *bledos* together with toasted maize, and after it was milled, kneaded it with honey, and made of that dough an idol." (See Appendix—B). The idol was carried on a litter in a great procession through the capital and the suburbs and then returned to the temple. At the close of the ceremony it was broken up, with other chunks of the same dough, and all the pieces were consecrated as the bones and flesh of Huitzilopochtli. The pieces were handed out to the populace and were eaten in communion with reverence, fear, and tears. On this day "it was a strictly observed rule in all the land that no other food was to be eaten except that dough with honey of which the idol was made. All those that participated were obliged to give a tithe of that seed of which the idol was made."

One of the most magnificent of the early chronicles was written about 1570 by Sahagún. This Spanish Franciscan compiled a monumental record of the language, beliefs, and ancient customs of the Indians of central Mexico, drawn from years of discussion and collaboration with groups of Indian informants. Over and over again Sahagún mentioned a ceremonial paste called *zoale*, or *"tzoalli,"* made of seeds of *bledos*. Idols of *zoale* appeared in at least seven regularly scheduled ceremonies and various irregular observances scattered through all seasons of the year (see table 1). Most of these rituals culminated in a ceremonial breaking and eating of the idols.

Sahagún confirmed the 'Ramírez Codex' account of a great idol made of *zoale* for the May festival to Huitzilopochtli, and described an almost identical ceremony in November:

> "They took seeds of *bledos* and cleaned them very well, removing the chaff and eliminating other seeds which they called *petzícatl* and *tezcahuauhtli*, and they milled them carefully, and after having them milled, the flour being very fine, kneaded it into dough of which was made the body of Huitzilopochtli" (see Appendix—C).

Sahagún identified *petzícatl* as the black seed of a plant called *quiltonilli*, which was sometimes cooked for greens. It and *tezcahuauhtli* may both have been weed amaranths (pl. 10 D-E). *Quiltonilli* is a common name for weed amaranths cooked for greens in central Mexico at the present time. This reference is of particular interest in suggesting that cultivated *huauhtli*, like most modern grain amaranths, was pale-seeded and, therefore, readily distinguishable from the dark-seeded weed amaranths. Sorting out the pale seeds from the dark seeds accidentally mixed in during the harvest is still common practice.

Zoale was not only used to make the idols of Huitzilopochtli but was also fed to slaves about to be sacrificed to that god. In a final midnight ceremony the temple fire was put out and in the darkness each slave was given four mouthfuls of a soup of *zoale* (see Appendix—C).

TABLE I

AZTEC FESTIVALS INVOLVING *HUAUHTLI* OR *BLEDO*, ACCORDING TO SAHAGUN (CA. 1570)

	Aztec month	Gods honored
February	1	
March	2	
April	3	
May	4—ueytozoztli	Chicomecoatl, goddess of crops
June	5—tóxcatl	Huitzilopochtli (Tlacauépan), war god
July	6	
August	7	
September	8	
October	9	
November	10—xócotlhuetzi	Xiuhtecutli, god of fire
December	11	
January	12	
	13—tepeilhuitl	Tlaloques, rain gods
	14	
	15—panquetzaliztli	Huitzilopochtli, war god
	16—atemoztli	Tlaloques, rain gods
	17	
	18—izcalli	Xiuhtecutli, god of fire
Variable date		Macuilxochitl (Xochipilli), flower god
		Omacatl, god of feasts

The fire god, Xiuhtecutli, was also honored by a formal and bloody ceremony, that of *xocotlhuetzi*. This also involved an idol of *zoale*, with *tortillas* of *bledo* seed on its head, which was tossed down from a tree, with the people scrambling for pieces (see Appendix—C). A slightly later chronicler, the Dominican friar Durán, attributed this festival to a non-Aztec group, the Tepanecs of Coyoacán:

> "The day of their festival they made a bird of dough of *bledo* seed which we have called *tzoalli*, which dough perpetually served them for effigy of idols and flesh and bones of their gods, that dough to be eaten afterward." (See Appendix—E).

Sahagún described another annual festival to the fire god in which amaranths may have been used, that of *izcalli*. All the women made *tamales* of *huauhtli*, or *huauhquilitl*, which they offered in the temple and in home ceremonies and also placed on the graves of their dead (see Appendix—C). These ceremonial *tamales* may have been made from vegetative parts rather than seeds. Sahagún identified *huauhquilitl* as *bledos* eaten as cooked greens and illustrated the young seedlings being gathered below a mature *huauhtli* plant (pl. 10 F).

The Tlalocs, mountain and rain gods, were honored by the formal ceremony of *tepeilhuitl*, by the milder household ceremony of *atemoztli*, and in irregular individual offerings when the weather required them (see Appendix—C). In all these rain rites, the centers of attention were anthropomorphic figures of the mountains fashioned of *zoale*. Sometimes *zoale* was also made into votive *tortillas* and smeared on tree roots and branches to represent snakes. Pomar (1582, p. 15) reported similar offerings to the Tlalocs at Tezcoco.

In the festival of *ueytozoztli*, an idol of the crop goddess was made of *zoale*. All the women presented ears of maize to her for blessing and took them home to keep for seed for the next year. She received offerings of maize, beans, and chia, because "she was the creator and giver of those things that are the sustenance of human life" (see Appendix—C). This ritual is strikingly like one practiced by the Tarascans in Michoacán, far beyond the limits of the Aztec empire (fig. 1). The Tarascans too had an earth goddess who was considered the mother of all the gods and the giver of grains and seeds (Anonymous, ca. 1540). For her festival at Tzintzuntzan, they made little figures of animals, called *tuycen*, of bread of *bledos*. When the Spaniards first came, the Tarascans called them gods and they called their horses *tuycen* (see Appendix—A).

Figures and offerings of *zoale* appeared again during the occasional festivals for the god of flowers and the god of feasts. Some persons mixed the flour of *bledo* seed with honey and meal of toasted corn for their offerings (see Appendix—C).

Finally, there was the new fire ceremony, held at the close of each 52-year calendar cycle. This rite insured the return of the sun for another 52 years; otherwise, the sun and earth would perish and horrible creatures would descend from the sky to devour all the people. A slow procession of priests, dressed as gods, marched to a particular hilltop, followed by an awed and silent multitude. There the new fire was kindled in a midnight ceremony. Torches lighted from the flame were carried by runners to all the waiting villages where people were gathered on the hills and house-tops watching for the first glimpse of light in the distance. When the torch-bearer arrived, everybody relit their fires, all of which had previously been put out. Their joyful celebration culminated in eating "*tzouatl*, which is food made of *bledos* with honey" (see Appendix—C).

Many other accounts of pre-Conquest ceremonies mention use of *huauhtli* or *bledos* (Durán, ca. 1580; see also Appendix—E; Acosta, 1591, p. 234; Torquemada, 1615, pp. 71–89; Serna, 1656, pp. 320–321, 357; Vetancurt, 1698, p. 86; Bancroft, 1875, 3:323; Bourke, 1892, pp. 523–525; Safford, 1917, pp. 286–289; Seler, 1927, p. 190; Bukasov, 1930, p. 149; Matschat, 1930, p. 26; Martínez, 1936, pp. 27–29). All these appear to be derived, directly or indirectly, from the 'Ramírez Codex' or Sahagún and will not be discussed here.

Colonial Period.—After the Conquest, ceremonial use of *zoale* was undoubtedly gradually suppressed by the church in its battle against heathenism and idolatry. Stubborn resistance by at least a few of the Indians is revealed by the writings of two 17th century priests. In 1629 Ruíz de Alarcón bemoaned the continuance of

idolatry in the Atenango district of Guerrero. His Indians persisted in making offerings to the devil with the first fruits of the *huauhtli* harvest; they milled these seeds and kneaded the dough into little idols of *zoale*, which they broke and ate in what seemed to the Spaniards a satanical parody of holy communion (see Appendix—H). Similar deviltry near Çumpahuacán in the Valley of Mexico was revealed "by confessions of certain delinquents" (Serna, 1656; see also Appendix —J). In various pueblos some old men retained the office of starting the new fire, and had preserved this great pre-Conquest ritual into the 17th century, complete with offerings of "*zoales*, which is a seed of *bledos*."

Recent.—Shortly before 1900 Lumholtz (1902, 2:47–50) visited the remote Huichol village of Haiokalita in the mountains of northern Jalisco and watched these primitive Indians celebrate their greatest feast of the year. Although he did not realize it, Lumholtz witnessed a ritual which was in some ways strangely like those practiced far off in central Mexico more than 300 years before:

> "In front of the drum was spread a blanket, and on this a great number of cakes were deposited, shaped to represent animals, such as the deer, turkey, rabbit, etc. They are made from a certain seed, which is ground and mixed with water. The seed, and the plant from which it is obtained, are called *wā-vē*; being yellow, it belongs to the god of fire. The tribe probably made use of this grain before they had corn. At present it is used chiefly for ceremonial purposes, except when the corn runs short. No one is permitted to eat it until the race is over."

The festival culminated in a ceremonial race for life; as each runner finished, he pierced a cake animal with a straw and handed it to one of the elders, who "in eating it secured health and life for all." *Wā-vē* was cultivated on a small scale by the Huichols and Lumholtz recognized it as a species of amaranth.

Farther south in Jalisco, where out-and-out pagan rituals have long since disappeared, grain amaranths have slipped into Christian ritual. In the late 19th century Edward Palmer visited an Indian village near Guadalajara and saw rosaries made of little balls of amaranth dough, called "*suale*", wrapped in maize husks (Safford, 1917, p. 293). In 1947 at Tlajomulco, another village not far from Guadalajara, we talked to a woman who was growing grain amaranths. She and her friends were accustomed to toast and mill the seed to make dough, which they called *zoale*. They made the dough into little ceremonial cakes and rosaries for something called the Feast of the Cat on December 8th.

The Tarascans of Michoacán, who made *tuycen* of *bledo* seed in pre-Conquest times, seldom use amaranths in ceremonies today, but in a few villages they make special *tamales* and *atoles* of black amaranth flour mixed with black corn meal for the maize planting and harvesting festivals (West, 1948, p. 42).

In the heart of the old Aztec Empire, no tangible vestiges of the once enormous ritual significance of *huauhtli* are known to remain. As will be discussed in the next section, the main modern use of grain amaranths in this region is for *alegrías*, little cakes of popped seed bound with syrup. These are in large part simply commercial confections, but for some reason they become particularly abundant and conspicuous on special saints' days.

HISTORY OF CULTIVATION AND ECONOMIC USE.—

The story of ritual use of *huauhtli* shows more clearly than any other evidence how deeply these plants were embedded in the memories and lives of various Mexican tribes. This is only part of the complete picture; beneath the colorful ritual usage lay a massive foundation of everyday practical use of the plants. This usage, not clearly the work of the devil, was largely ignored by the early Spanish writers; fortunately, it was recorded by the Mexicans themselves. Some of the Mexican hieroglyphic codices from before and after the Conquest are still in existence. As their deciphering has progressed, there has been gradual realization that they record not only rituals and myths, but also a great deal of historical fact (Caso, 1949, p. 145).

Pre-Conquest.—Some of these records were exploited very early by the native historian Tezozomoc (ca. 1598). His history of the Aztecs before the Conquest undoubtedly involves errors and fantasies, but its credibility probably differs only in degree from most ancient history. Tezozomoc described the centuries of tribal wanderings down from the Northwest until the final settlement at Tenochtitlán. The tribe settled at many places and planted and harvested their crops, often remaining for many years until their god Huitzilopochtli bade them move on. Even in the earliest legendary times, *huauhtli* was among their crops; being light, the seed was carried by the boys whenever the tribe migrated (see Appendix—G). When the tribe settled at Xaltocan, *huauhtli* was sown in beds in the lake, like the "floating gardens" at San Gregorio Atlapulco in which amaranths are grown today. Acosta (1591, pp. 303–304) recounted another Aztec legend from these early times: Huitzilopochtli helped the tribe pay a crushing tribute, including *bledos*, to the king of Atzcapotzalco.

Tezozomoc narrated mostly events of the 15th century. When the Aztecs conquered the Tepanecs of Coyoacán, the vanquished tribe ran up on a hill and shouted down pleas for mercy, promising all sorts of tribute, including *huauhtli* "for your sustenance" (see Appendix—G). During the reign of the first Moctezuma (spelled Montezuma in popular English writings) and his successor, Axayacatl, both pale- and dark-seeded *huauhtli* was stocked in the imperial larder and was given as a reward, "with the other things pertaining to the necessities of their houses," to persons who had earned the gratitude of the emperor (Tezozomoc, ca. 1598, pp. 152, 161, 237). Later in the century, *huauhtli* was stated to be one of the four food crops of the Matlazincas in the valley of Toluca and was supplied as food to a Mexican colony at Teloloapan in Guerrero by the neighboring pueblos (see Appendix—G).

A wealth of definite information on the Aztec Empire just before the Conquest is available in Moctezuma's tribute list, the famous hieroglyphic 'Matricula de Tributos.' From this document Barlow (1949) has mapped the provinces of the empire and summarized the tribute levied on each province. *Huauhtli* was collected from all but three of the twenty provinces which contributed food staples. Each

of these seventeen provinces filled at least one granary with *huauhtli* every year, and some were required to fill two. A single granary is believed to have held about 10,000 bushels of seed (Gallatin, 1845, p. 117; Safford, 1917, p. 286; Bukasov, 1930, p. 149; Anderson and Barlow, 1943, p. 416). Thus the annual levy of these tiny seeds added up to something like 200,000 bushels, a staggering total not far exceeded by any foodstuff. Computed on the same basis, the maize tribute was about 280,000 bushels and the bean tribute about 230,000 bushels. It is obvious from these figures that *huauhtli* was one of the great basic food crops of the empire.

The provinces submitting *huauhtli* tribute cover the heart of the empire (fig. 1A). It may be significant that some provinces in the present states of Puebla and Oaxaca contributed maize and beans but not *huauhtli*. No significance can be attached to the absence of *huauhtli* in the tribute of the rest of the empire, since the more distant provinces did not contribute basic foodstuffs of any kind.

Colonial Period.—For a long time after the Conquest, the Spanish chroniclers seem to have completely ignored the more prosaic aspects of this great crop. Núñez Cabeza de Vaca (1555, p. 513), who had made a fantastic journey through the far northwest of Mexico in the 1530's, made a puzzling statement that "the coast has no maize and they eat powder of *bledo* and of straw and of fish." This cryptic remark has sometimes been taken as a reference to cultivated grain amaranths, which have been reported from this general area in recent times. However, it seems probable that in this particular passage Cabeza de Vaca was describing the territory of the non-agricultural Seri tribes (Carl Sauer, 1932, pp. 16–17). If so, the "powder of *bledo*" may have been made from wild amaranth seeds.

The first definite post-Conquest record of *huauhtli* as a crop and everyday foodstuff was made by Sahagún. There is some evidence that Sahagún's original manuscript contained an extensive account of cultivation and use by the Aztecs of *huauhtli* and other crops. This section is not included in any of the available versions of the work. However, in another section Sahagún reports *huauhtli* among the staple food crops of two non-Aztec peoples: the Matlatzincas of Toluca and the Tarascans of Michoacán (see Appendix—C).

Francisco Hernández, contemporary of Sahagún and physician to the King of Spain, spent several years in Mexico preparing a catalogue of its natural history. His completed manuscript has been lost, although modified abstracts of it prepared by Ximénez (Hernández, ca. 1575a) and Recchi (Hernández, ca. 1575b) are preserved. Probably the most authentic version, quoted here, is that published by Ortega (Hernández, ca. 1575c) from the original rough draft, rediscovered in the 18th century. Hernández wrote that there were many kinds of plants called *huauhtli*, some wild, some carefully cultivated in the gardens of the Mexicans (see Appendix—D). He mentions various long Indian names applied to particular kinds, but makes no clear distinction between them other than coloration. The only use mentioned for most of the kinds was as boiled greens; some of these were probably chenopods, as has already been mentioned. However, from the seeds of

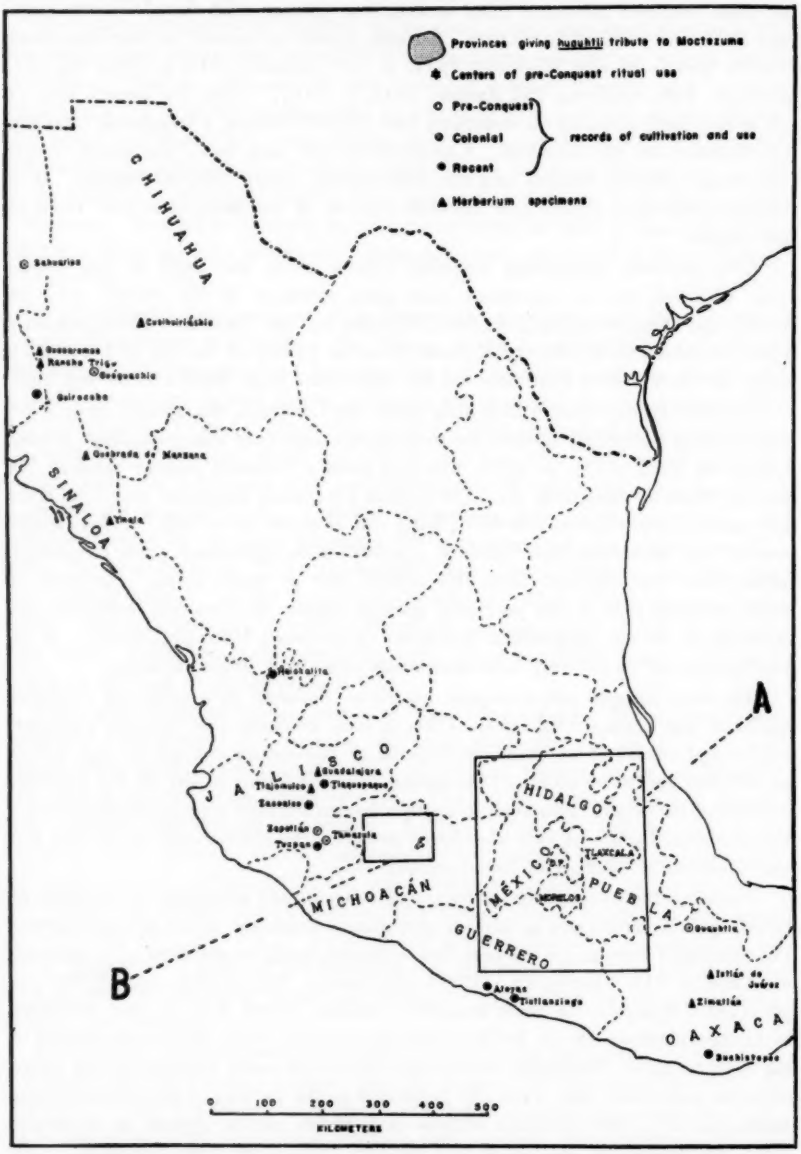

Fig. 1. Mexico: Localities and regions where grain amaranth cultivation is indicated; enlargements of squares A and B on opposite page.

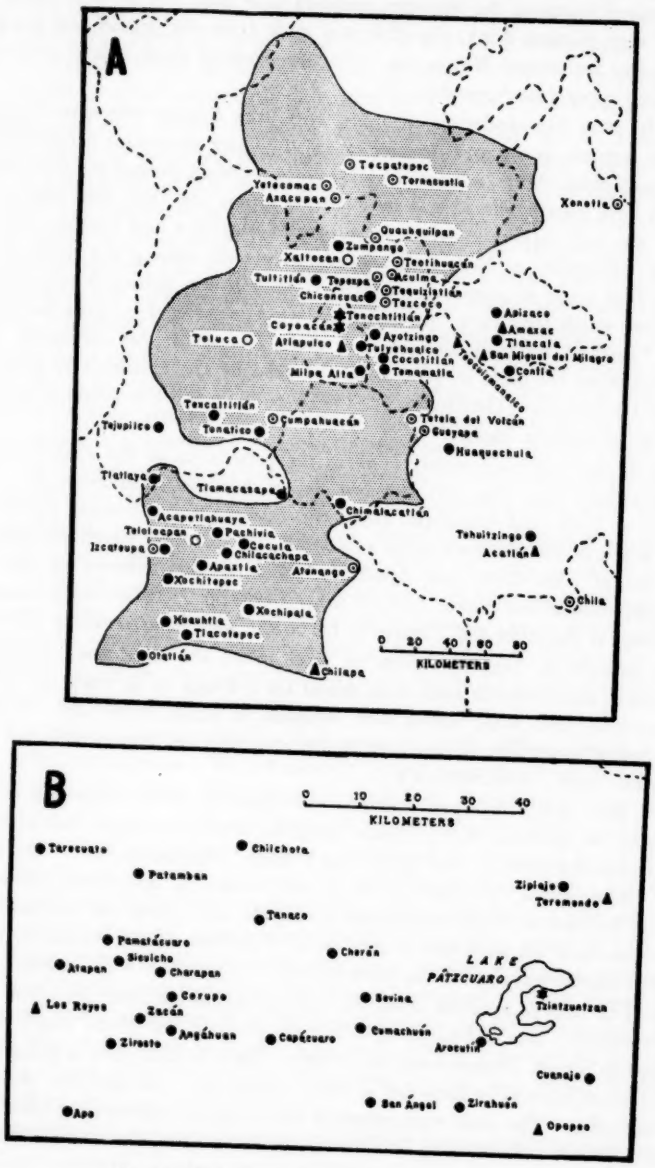

Fig. 1A. Enlargements of squares shown on fig. 1.

a few kinds of *huauhtli*, the Mexicans prepared little balls and an *atole* which was used as a very pleasant drink; the *atole* was made from the toasted and powdered seed of red or varicolored *Blitum*, the Latin equivalent of *bledo*, mixed with water and maguey syrup (see Appendix—D).

Shortly after Hernández finished his work, the famous *relaciones* began to appear, in response to the royal inquiry of 1577. These documents often included, among many other things, a listing of local crops. Only a limited number of these *relaciones* have been published and are available to me, but they show clearly that *huauhtli* was still important over a large part of Mexico a half century after the Conquest. *Huauhtli* or *bledo* seed appeared repeatedly among the three or four standard food crops of particular pueblos; at some it was described as an ancient crop or one which they have "always" had (see Appendix—F). One mention of seeds of "*quilites*" probably also refers to grain amaranths; this corruption of an old Nahua word for herbs in general was adopted by the Spanish very early as a synonym for *huauhtli* (Hernández, ca. 1575a, p. 235) and is a common name for amaranths in modern Mexico.

Most of the *relaciones* merely confirm the persistence of the crop in the old *huauhtli* tribute area (fig. 1), but two report *huauhtli* cultivation far to the southeast at Chila and Guauhtla, along the Puebla-Oaxaca border, and another gives it as one of the two main crops at Xonotla, far off to the northeast, nearly on the border of Vera Cruz (see Appendix—F). Another *relación* of this same period, unpublished but quoted by Carl Sauer (1948, p. 75), lists *zoale* among the major crops at Zapotlán and Tamazula, far to the west in present-day Jalisco.

The *relación* of Tezcoco reports in more detail the same uses described by Hernández: dark *huauhtli* seeds were milled for a dough to be made into tortillas or rolled into little balls, which were wrapped in maize leaves and boiled; the whitish *michihuauhtli* seeds were used in the same way and also toasted and milled for a sweet drink (Appendix—F).

Fifty years later, cultivated *huauhtli* was observed around Atenango in Guerrero (Ruíz de Alarcón, 1629). Here again the seeds were made into little *zoale* balls, cooked like *tortillas*, and made into a drink (Appendix—H). Toward the end of the century, Vetancurt ,1698, p. 45) wrote an apparently garbled and secondary account in which amaranths, chenopods, and salvias are confused. This account mentions the same sort of uses and is of interest mainly because it contains the first available mention of the name *alegría* in connection with *huauhtli*.

The final records available from the colonial period are from far off in northwestern Mexico. One document described the crops of the Jovas, who lived near Sahuaripa in Sonora (Anonymous, ca. 1760). These Indians grew a plant, known to them as *coguet*, to the Mexicans as *zoale*, which had a pale seed like *quelite* (see Appendix—K). The seeds were prepared for eating by submerging them in the river in a basket and stamping on them under water until they burst; they were then toasted, milled, and stirred into cold water to make a refreshing drink. The other document is an unpublished manuscript on the isolated Tarahumare pueblo

of Guéguachic in Chihuahua (Anonymous, 1777). These primitive Indians sowed a seed resembling sesame which they called *oguigui* and the Mexicans called *alegría*. It was planted in August in the warm gorges and harvested in November. "When toasted it pops and swells greatly, and is of very good flavor." The popped seed was eaten dry or milled and mixed with water for a drink (see Appendix—L).

Recent.—In the 1890's the Mexican government sent out an agricultural questionnaire, which, like the royal inquiry of 1577, requested a listing of local crops. A comparison of the replies to these two inquiries shows that the three intervening centuries brought many changes in Mexican crops, none more striking than the decline of grain amaranths. The replies to the later inquiry cover a great number of pueblos, including some where *huauhtli* was a major crop about 1580. Although the crop lists are often quite long, not a single one mentions grain amaranths (República Mexicana, Secretaría de Fomento, 1893–1895).

Planting and use of *huauhtli* was one of the ancient practices which suffered most heavily in the general disruption of Indian cultures. The very importance and ceremonial value attached to the plant in the old days worked against its survival by making it a symbol of paganism in the eyes of the church. The decline of the crop was reflected by its increasing rarity in late colonial records; by early post-colonial times it seems to have disappeared completely from written history.

In modern times, with the beginning of intensive botanical and ethnological field work, grain amaranths have been rediscovered in many parts of Mexico. Although reduced to an inconspicuous relic of the once great staple, the crop has been conserved by a surprisingly large number of Mexican communities. Sizeable fields of amaranths are planted by only a few pueblos today; generally a few plants are sown near the houses or scattered through the maize fields; often only a small minority of the families still grow them.

A crop grown on such a small scale can easily escape notice, even in a fairly careful field investigation. We occasionally found persons who had patches of amaranths in pueblos where other inhabitants had said, and probably believed, that none were being grown. Although the crop has undoubtedly disappeared in many communities, it probably persists in many more than are indicated by the known present distribution (fig. 1). On a trip through Mexico lasting only a few weeks, we found cultivated amaranths in several areas where they had not been previously reported. Additional field investigation could be expected to round off and fill in the distribution pattern. For example, it is quite possible that there are spots of amaranth cultivation scattered along the almost unexplored western Sierra Madre, which would link the apparently isolated northwestern centers to the main range. However, there is no reason to expect grain amaranths to turn up very far outside the known range; most of the large blank areas on the map persist in spite of traverses by persons interested in the plants.

For convenience, the post-Colonial records will be discussed by states.

Federal District, State of Mexico, and Morelos.—Grain amaranths remain a more important crop in this area, the heart of the old Aztec Empire, than in most of the rest of Mexico. Some pueblos continue to make large-scale plantings, mostly to supply the demand for the popped *alegría* confections. Almost any kind of amaranth seed will pop when toasted, but the kind grown in this region puffs up to an unusually large size, suggesting long selection for this character. The practice of using unmilled popped seeds cannot be traced very far back with any certainty, but the seeds have been toasted and presumably popped for as long as there has been any record, so that selection for popping quality may be very ancient.

Detailed accounts of techniques of cultivation and *alegría* manufacture in the state of México were prepared in the 1880's in response to a government request (Granados, Noguerón, and Zarza, 1886). At that time the crop was grown extensively at Cocotitlán and Temamatla and on a small scale at Ayotzingo. Three different kinds of seed were distinguished: *quitlacoche* was small and black and was regarded as an inferior wild kind; *ojo de pájaro* was larger and pale; *cacahuacentle* was the largest and palest. The name *cacahuacentle* is shared with a variety of maize with especially large white kernels (Anderson, 1946, pp. 166–167). All three were often mixed in sowing and harvesting.

Planting began with the start of the rainy season in late April or May. The fields were prepared just as for maize, but instead of being planted along the bottom of the plow furrow, the amaranth seed was sprinkled into a tiny furrow drawn along the plow ridges with a stick, and was lightly covered with a broom. The seedlings were thinned and the excess transplanted, leaving well-spaced pairs of plants. As the plants grew, the earth was hilled up around them by repeated plowing until the stems were covered to a depth of about 30 centimeters. Bloom began in August, and in late October or November the seed-bearing tops were cut and piled in windrows in the fields to dry. After threshing with horses or by beating with sticks, the seed was cleaned by a series of special screens.

The seed was sometimes milled for dough, but the main use was for commercial *alegría* manufacture. The confections were made from December through May, after which the weather became too damp for the sugar binder to hold the cakes together. The seeds were moistened in a clay pot for a few hours and then spread on a cloth until partly dry before they were toasted. The popped kernels were mixed by hand with partly caramelized syrup and spread on a tule mat; the mixture was then compacted "with the greatest violence" into a sheet about 8 centimeters thick, from which little squares were cut with wooden knives. These cakes were sold locally or in the nearby city of Tezcoco.

More recently, the crop was reported a little to the west at Tulyehualco and Milpa Alta (Martínez, 1925, p. 27; Bukasov, 1930, p. 149), and it is extensively grown in this region to the present day (see pl. 11). Cultivation and *alegría* manufacture remain essentially as described in 1886. However, at San Gregorio Atlapulco the seed is often sown in March in the lowland *chinampas*, the so-called

floating gardens; thus the plants are well started before the rains begin, when they are transplanted to the upland fields. We were told that the crop is exhausting to the soil and is usually heavily fertilized and rotated with maize. The seeds, almost all pale, are made into *alegrías* in the individual households; the confections are peddled locally or in nearby towns.

Small-scale amaranth cultivation and *alegría* making are also carried on a little farther north at Chiconcuac and Tultitlán (Kelly, letter) and Zumpango (Hendrichs, letter), and also to the south and west of this region at Chimalacatlán, Tejupilco, Tlatlaya, Tonatico, and Texcaltitlán (West and Weitlaner, letters). At the last three places the seeds are sometimes milled to make dough and *atole*.

Guerrero—Grain amaranths are still sown in the maize fields in the rough mountain country of northern Guerrero, although their cultivation seems to be declining (Hendrichs, 1945, 1:35). Hendrichs wrote me that it is his impression that the custom of sowing a little *alegría* has persisted quite generally throughout these mountains. He particularly remembers the plants at Xochitepec and at Iscateupa, where seeds of *quelites* were an important crop in 1579. The mature inflorescences are cut and threshed on mats; the seeds, mostly pale, are popped over a *comal* and milled in a special non-porous *metate* for *atole* (Hendrichs, 1945, 1:35).

The crop survives in other parts of the state also. Hernández X. found a pale-seeded amaranth in cultivation at Chilapa and collected seed which I have grown. At Xochipala pale-seeded *alegría* is planted in the moist canyon bottoms and the seed is ground and mixed with sweetening to make little balls (West, letter). Weitlaner wrote me that he has unpublished records of *alegría* or *bledo* cultivation at a dozen other Guerrero pueblos, two of which lie well to the south of the old *huauhtli* tribute area (fig. 1). At only a few of these places are the plants carefully cultivated; usually the plants are sown in the maize fields or in newly-cleared ground; at Tlacotepec the plants are said to seed themselves. The seeds, mostly pale but sometimes dark, are commonly toasted over the *comal* and milled for *atole; alegría* confections, sometimes called *palanquetas*, are made here and there; *bledo* seed is milled for *tortillas* at Atoyac.

Tlaxcala and Puebla—All of Tlaxcala and much of Puebla were independent of the Aztec Empire and therefore excluded from the tribute list. However, the 16th century reports of the plants at Gueyapa and Chila and their scattered present distribution (fig. 1) suggest an old and once widespread crop.

In 1947 we saw cultivated amaranths at the Tlaxcalan village of San Miguel del Milagro. Three plant color forms are distinguished but are not kept separate; all are pale-seeded. The plants are started in January or February in seed-beds protected from frost and are transplanted to unirrigated upland fields, either in solid stands or mixed into the maize plantings. The seeds are harvested in September and made into the popped *alegría* confections, especially for the feast of the patron saint, Michael, on September 29.

In 1948 Hernández X. collected a predominantly pale-seeded amaranth cultivated for *alegría* making at another Tlaxcalan pueblo, San Bernabé Amaxac; he has observed cultivation at several other pueblos in the state (fig. 1).

In 1947, travelling south through Puebla, we heard the first rumor of grain amaranths near Huaquechula; *alegría* was said to be cultivated off in the hills at a village called Santa Clara Tetla. Weitlaner has also heard that *alegría* is grown near Huaquechula; at a place called Santiago Tetla the seed is said to be accumulated in quantity in large baskets and made into a confection, called *palanquetas*, with caramel syrup or bee honey.

Later we found a few people growing pale-seeded *alegría* for confection-making at Acatlán; they said that the people of Tehuitzingo also grew the plants. The next year Carl Sauer obtained pale-seeded *alegría* from plants cultivated atTeocuizmanalco in the northern part of the state.

Oaxaca—After the single 16th century report from Guauhtla, Oaxacan grain amaranths seem to vanish from the record until Erwin (1935, p. 661) noticed the popped *alegría* confections for sale in the markets of Oaxaca City. In 1947 we found the confections were still on sale in the city markets; they were made locally from seed said to be brought from Ixtlán de Juárez and Zimatlán. The samples we obtained were mostly pale, but a few dark seeds were mixed in.

We could find no other trace of the plants on a traverse of the state, but a suggestion that they may be scattered through some remoter areas is given by the presence of amaranth cultivation and *alegría* making at San Miquel Suchistepec (Hernández X., letter).

Michoacán—Here in the old Tarascan Empire, the unrecorded story of grain amaranths may have been much like it was in the better-known Aztec Empire. We know that in the 16th century *huauhtli* or *bledo* seed was used ceremonially at Tzintzuntzan and was an important Tarascan food crop. After that the story is lost for centuries until the crop was rediscovered by modern field workers. In its uses and distribution the present crop looks very much like a relic of something more widespread and important.

West (1948, p. 42) says: "The cultivation of amaranth is disappearing among the Tarascans; it would probably die out rapidly if women did not constantly remind men to plant it every year." He found that many pueblos which no longer grow amaranths still use the seed, brought in from mountain villages.

Cultivation continues in quite a few Tarascan and *mestizo* villages (fig. 1). Most of these locations are based on West's records and seed collections, which he has permitted me to grow; the only other recent records are from Cherán and Chilchota (Beals, 1946, p. 52; Weitlaner, letter). I looked for grain amaranths in Tzintzuntzan in 1947, but could find only plants grown as greens or ornamentals.

The Tarascans distinguish varieties on the basis of seed color; they are mixed in planting and the seeds are sorted by color after the harvest (West, 1948, p. 42). Grain amaranths are known as *pari* in Tarascan and as *alegría*, *bledo*, or *quelite* in Spanish (Beals, 1946, p. 52; Rendón, 1947, p. 223; West, 1948, p. 42). The seeds

are planted in small patches in the house-lot gardens or in the maize fields, particularly in spots where logs have been burned. Sowed in late May, the crop is harvested in November and December; the grain is threshed from the cut inflorescences in open spaces in the fields and stored in small pots (West, 1948, p. 42).

The black seeds are sometimes ground with black maize for *atole* but are mostly used in making *tamales*, locally called *chapatas*. These are made from a mixture of black *bledo* seed, red chenopod seed, and blue or black maize flour; water and sweetening are added to make a dough, which is wrapped in maize husks and cooked in a clay pot (Beals, 1946, p. 52; Rendón, 1947, p. 223; West, 1948, p. 42). Beals also saw *chapatas* made solely of black amaranth dough and brown sugar; the raw paste was spread on banana leaves and eaten at festivals.

The white seeds are mostly popped on a *comal* and made into *bolitas*, sweet confections commonly sold at fiestas, particularly in the mestizo towns (West, 1948, p. 42). Rendón (1947, p. 223) reports that these confections are peddled by the Indians, who make them from the produce of their own plants.

Jalisco—In 1886 Edward Palmer found grain amaranths at Guadalajara and collected herbarium specimens which are still available. The plants were cultivated alone or in the maize fields; the pale seeds were parched and sprinkled with honey to make *alegrías* to be sold in the city market (Watson, 1887, p. 446). At a nearby Indian village, Palmer saw little balls, called *"suale"*, made from ground amaranth seed and brown sugar (Safford, 1917, p. 293). At about the same time in a more remote part of northern Jalisco, Lumholtz observed small-scale amaranth cultivation among the Huichols. There the plant and its pale seeds were known as *"wã-vë."* As we have already seen, the seeds were usually eaten ceremonially, but they also served as ordinary food when maize was scarce (Lumholtz, 1902, 2:48).

More recently grain amaranths have been reported from Tlajomulco, Tlaquepaque, Zacoalco, (Bukasov, 1930, p. 149), and from Tuxpan (Weitlaner, letter), a town where *zoale* was a 16th century crop. In 1947 we saw small patches of grain amaranths in house gardens at Tlajomulco. Sown when the rains begin in May, they are harvested in December. The inflorescences are cut, dried in the sun for a few hours and then rubbed between the palms of the hands to free the seeds, which are cleaned of chaff by blowing. The predominantly light-colored seeds are toasted and milled to make *zoale* cakes; these cakes are primarily ceremonial, as has been mentioned, and are of minor importance as food.

Sonora, Chihuahua, Sinaloa—In 1891 Edward Palmer collected specimens of a grain amaranth at Ymala; the plants were called *bledos*, the seeds *"guaute."* The pale seeds were much used for food, particularly when maize was scarce, and the plants were sown or allowed to seed themselves in the maize fields (Safford, 1917, p. 292).

Some puzzling amaranths, perhaps representing a grain crop, were collected by Wislizenus at the remote village of Cusihuiriáchic, Chihuahua, in 1846. For

some reason, Engelmann planted seed of this collection at St. Louis a year later from which he obtained an additional herbarium specimen. These collections are accompanied by no data on habitat or use, but the plants are completely unlike any of the known wild amaranths of this region and almost identical to Palmer's grain amaranths from Ymala.

In the remote canyons of the Sierra Madre off to the west of Cusihuiriáchic, grain amaranths have recently been discovertd by Gentry (1942, p. 108). He collected plant specimens at Guasaremos and Quebrada de Manzana and sent me viable seeds from Rancho Trigo (fig. 1). The plants are cultivated in the house gardens of the Warihio Indians and a few plants are often seen around the houses of the Mexicans (Gentry, letter). The pale seeds are eaten whole or ground into *pinole*, which is mixed with water or milk, sometimes sweetened, to make a drink. The Mexicans call the plants *quelite* or *bledo;* the Warihios call them *weywi.* Carl Sauer recollects seeing large quantities of *bledo* or *guegui* seed stored at Guirocoba, the produce of plants cultivated by the Mayo Indians, neighbors of the Warihio. All the names *(oguigui, guegui, weywi, wā-vē)* for this crop among the various Indian tribes of northwestern Mexico are probably merely variants of a single name.

GUATEMALA

If there are any ancient records of grain amaranths in Guatemala, I have been unable to find them. Even in recent literature, the only published reference to the plants seems to be the single statement that around Cobán the seeds of an amaranth are mixed with brown sugar to make a confection (Standley and Steyermark, 1946, p. 154). The crop is practically unknown to everybody except the Indians who grow it. After travelling halfway across the country and questioning not only Indian farmers but also professional botanists and ethnologists, I had drawn a complete blank and was convinced there were no such plants in Guatemala. Finally the ethnologist Rodas, a Quiché Indian himself, told me about cultivation at San Martín Jilotepeque. On the way out there, the bus driver, a part-time farmer who had driven the route for years, assured me that nobody grew any such plants in that area. When I pointed out some of the big gaudy red plants in the maize fields along the road, he stopped the bus to get out and look at them, and was astonished when the local people confirmed my strange notion that the seeds were good to eat.

I saw grain amaranths at only three places, in the departments of Chimaltenango, Guatemala, and Alta Verapaz, and heard definite reports of cultivation at only two other villages, both in Chimaltenango (fig. 2). Two amaranth specimens from elsewhere in Alta Verapaz may well represent grain plants. They were collected without information on uses, but belong to races ordinarily grown for grain. One, with dark seeds, was found in a maize field at Cubilquitz by von Tuerckheim in 1903; the other with pale seeds was collected in an unspecified habitat near Secanquim by Pittier in 1905.

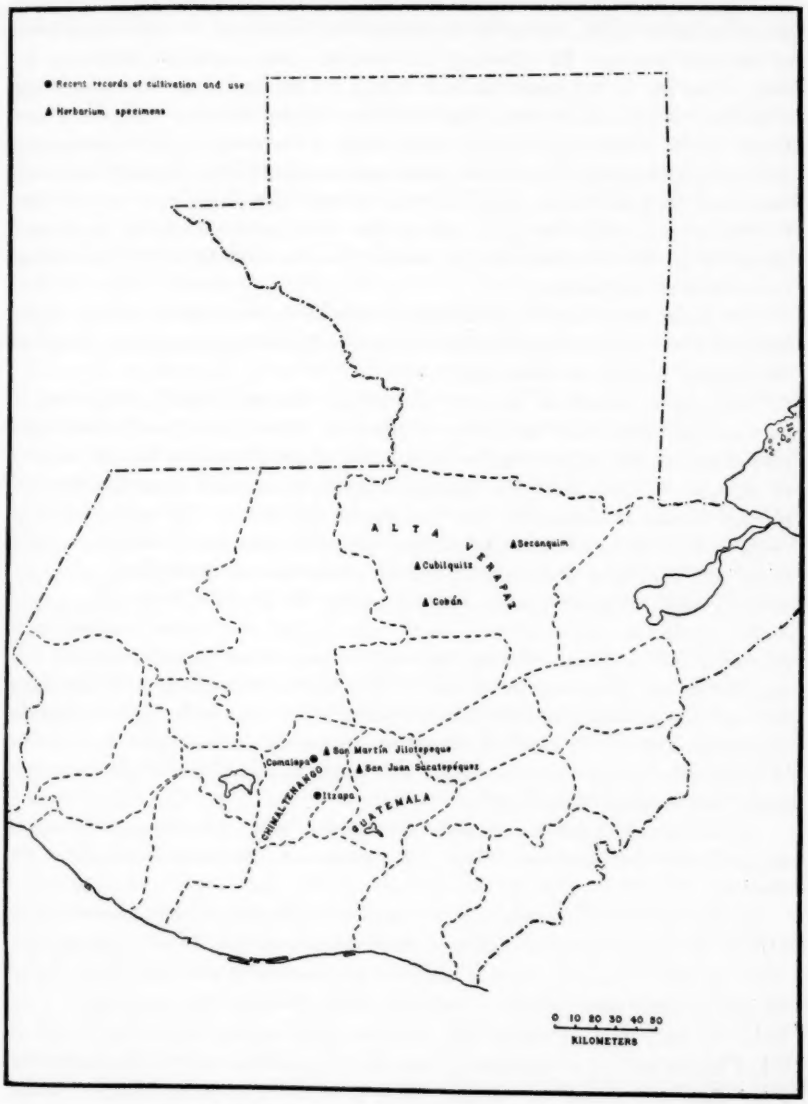

Fig. 2. Guatemala: Localities and regions where grain amaranth cultivation is indicated.

Wherever I saw the plants, I was told that the crop was much more important, grown in entire fields, among the uncivilized Indians far off in some vague areas of the back country. The plantings seen were on a very small scale and made by only a fraction of the people in each village. They said that they grew large quantities only as a catch crop when maize was scarce; usually a few plants were grown in the house lots or in the maize fields. The seeds are often sown in a new burning or in heavily manured ground and occasionally the plants are irrigated. Sometimes the plants were simply allowed to seed themselves from year to year. I talked to one Indian for quite a long time while he was chopping weeds and hilling his maize, and noticed that in several places he carefully avoided disturbing some volunteer amaranths.

The plants are generally called *bledo* in Spanish or some variant of *tez* in the Maya dialects. Varieties are distinguished on the basis of plant and seed color, but are not kept separate in cultivation.

The crop is planted at the start of the rainy season in April or May and is harvested gradually from September to January. Much of the seed is made into popped confections, bound together with brown sugar syrup, just like the *alegrías* of Mexico. In Guatemala, they are called *niguas*, the Spanish name for chiggers, perhaps because the seeds look like tiny insects (pl. 12B). The paler seeds pop better and are preferred for *nigua* making, although some black seeds are usually mixed in. Popping is done in small batches in the huts of the farmers, using the family *comal*. Sorghum seed is often popped by the same people to make a very similar confection called *alboroto*, and some hybrid confections include both amaranth and sorghum. During the drier season, when the cakes do not fall apart from the dampness, the people of San Martín Jilotepeque and San Juan Sacatepéquez peddle *niguas* and *alborotos* quite widely in the Antigua-Guatemala City area. Lots of the people who told me that no grain amaranths were grown in Guatemala had known about *niguas* all their lives, but they thought they were made from sorghum, like *alborotos*.

In Cobán cultivation is extremely inconspicuous and confections, called *jaleas*, are made only for home use. There the seeds are usually toasted and milled for *pinole*.

In San Martín Jilotepeque and San Juan Sacatepéquez, in addition to making *niguas*, the people prepare the seed in various ways for home consumption. Although they regard the seeds as healthful and nutritious, they seem to be rather apologetic about these practices; maize obviously has more prestige value. They make the seeds into a gruel or mill them for flour, which, with sugar added, is baked into bread. More commonly, however, they soak the seeds in hot water and grind them into dough for *tortillas*, alone or mixed with maize dough. White *bledo* seed is preferred for tortillas, but the black seeds are commonly used, since they are not acceptable for anything else.

PERU AND BOLIVIA

Records of grain amaranths in European herbals are of little value in the case of the North American races; they cannot be recognized in European botanical literature until centuries after the Conquest (Thellung, 1914, p. 236). In contrast, one of the South American grain amaranths, eventually named *Amaranthus caudatus* by Linnaeus, entered Europe very early as an ornamental plant. It can be traced through various late 16th century herbals (Thellung, 1914, p. 232), usually with no place of origin specified, until Clusius assigned it to Peru. Clusius apparently obtained some sort of evidence that the species was a South American grain crop; he presents a good illustration of the plant labelled "*Quinua, sive Blitum majus Peruanum*" (1601, Lib. 4:81). Clusius assumed that this was the same crop as the *quinoa* found in Ecuador by Pedro Cieza de León, which was undoubtedly a chenopod. This confusion is natural, since the name *quinoa* has often been used ambiguously for grain chenopods and amaranths and is still applied to both in parts of South America today. Linnaeus (1737, p. 443) cited Clusius in describing the same species and agreed that it came from South America.

In contrast to Mexico, the historical record of grain amaranths in the Andes is extremely poor. One reason may be that in western South America the activities and settlements of the Spanish colonists were concentrated on the coast, rather than in the highlands to which grain amaranths are almost invariably confined. Also, in the Andes grain amaranths may always have been a minor and localized crop, easily overlooked or confused with the similar and much more abundant grain chenopods.

The tremendous ceremonial role played by *huauhtli* in the Aztec Empire was taken over by maize in the Inca Empire. The Inca Feast of the Sun was in some ways startlingly like the Aztec feast of Huitzilopochtli. It too was the greatest feast of the year, held in the capital city with bloody sacrifices and colorful processions of all the chiefs and dignitaries. Just as in Mexico, the temple maidens on the night before the feast prepared a sacred bread, to be distributed and eaten ceremonially, but in Cuzco the bread was of maize (Means, 1931, pp. 368–372).

Thanks to the Jesuit chronicler Cobo (1653), there is one record of grain amaranths in colonial Peru. He distinguished *bledos* from *quinoa* and wrote that red and white *bledos* were "very common food of the Indians, and in the city of Guamanga (fig. 3) very pleasing candies are made of the seed of the white *bledos* and sugar" (See Appendix—I).

Until the present century no further notice of this crop seems to have been taken by anyone but the Indians. Finally Thellung (1914, p. 233) published a report by Spegazzini that the Chiriguano Indians around Tarija in Bolivia cultivated a white-seeded amaranth under the name of *Inca-pachaqui*, or Inca grain; they ate the seeds as meal or grits. In 1915 O. F. Cook collected a pale-seeded amaranth, called *quihuicha*, in the Urubamba Valley of Peru near Ollantaytambo. Cook later wrote that *quihuicha* was grown as a seed crop in the temperate valleys around Ollantaytambo and that the seeds popped like Indian corn (1925, p. 36).

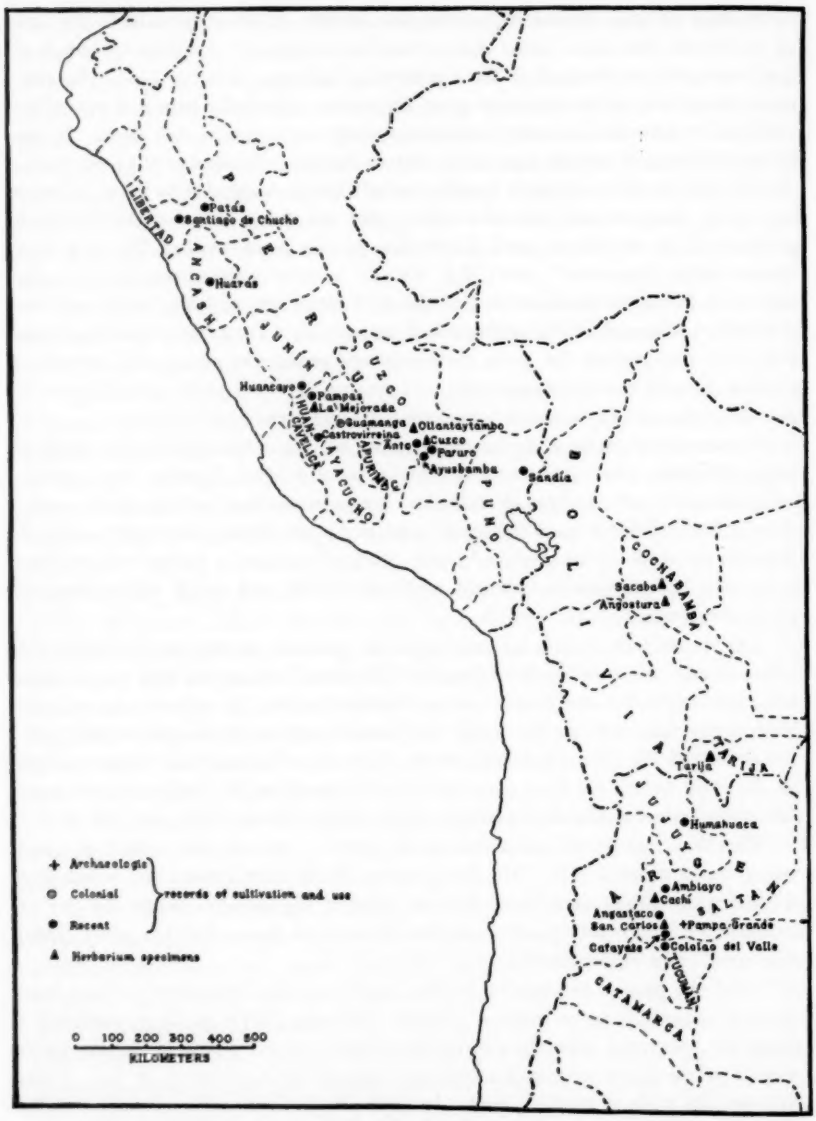

Fig. 3. South America: Localities and regions where grain amaranth cultivation is indicated.

At about the same time, Weberbauer found the plants growing near the Indian houses quite widely through the department of Cuzco (Herrera, 1921, p. 74).

In recent years the crop has been observed by botanists in various parts of Peru and Bolivia. In Peru it is reported at Patás and Santiago de Chucho in Libertad, at Huarás and the Callejon de Huaylas in Ancash, at Huancayo in Junín, at Castrovirreina, Pampas, and La Mejorada in Huancavelica, at unspecified places in Ayacucho and Apurimac, at Anta, Paruro, and Ayusbamba in Cuzco, and at Sandía in Puno (Herrera, 1940, p. 229; Hunziker, 1943b, pp. 338–339; Weberbauer, 1945, p. 619; Pulgar Vidal, 1946, 1:115; Arévalo, Cárdenas, and Rick, letters). In Bolivia the crop has recently been reported in Tarija where it was first found by Spegazzini, and also in the department of Cochabamba (Hunziker, 1943b, pp. 337–339). Cárdenas and Cutler have supplied me with seed collections from Sacaba and Angostura in Cochabamba.

Herrera believed the plant was an important ancient, possibly pre-Inca crop of the temperate valleys of Peru, which has declined to a relic in recent times (1940, p. 229). Pulgar Vidal (1946, 1:115) reported that it was an ancient widespread crop of the highlands, "but it is unknown in the city markets, its consumption being limited to the small harvests that each person obtains from the fringes of the maize fields." Other persons who have seen the crop in Peru agree that it is grown only by the Indians in small plantings on the edges of the maize fields (Weberbauer, 1945, p. 619; Rick, letter).

Cárdenas gives a similar picture for Bolivia. He wrote me that the grain amaranth "is becoming a very rare and odd foodstuff", and later (1949, p. 115) described it as an "autochthonous cultivated species on the road to extinction." As in Peru, the plants are not grown in pure stands, but are sown along the edges of the maize fields.

Both the Peruvian and Bolivian plants used for grain are mostly pale-seeded, but some dark seeds are usually mixed in. The seeds are prepared by toasting, parching, or popping; they are commonly eaten alone, sometimes in milk or in stews or mixed with other flour (Pulgar Vidal, 1946, 1:115; Arévalo, Cárdenas, Rick, letters).

The name *quihuicha* seems to be used only in the Cuzco area. Elsewhere in Peru the plants are called *achis, achita, ckoito, coyo,* or *coimi;* in Bolivia they are called *coimi, cuime, millmi* or *quinua millmi* (Cook, 1925, p. 99; Herrera, 1940, p. 229; Hunziker, 1943b, pp. 331–339; Weberbauer, 1945, p. 619; Pulgar Vidal, 1946, 1:115; Cárdenas and Hawkes, 1948, p. 31; Arévalo, Cárdenas, letters). In both countries, weed amaranths are given a different name than the grain crop, usually some variant of *jataco.*

ARGENTINA

In an archaeologic site, believed to be pre-Columbian, at Pampa Grande in the Argentine province of Salta, a funerary urn full of seeds was recently unearthed. Mixed in with maize, bean, and chenopod seeds were a quantity of

amaranth flowers and pale seeds, identified as *A. caudatus* by Hunziker (1943a). Since this species is unknown in a wild state, this discovery is good evidence that the crop is ancient in the northwestern Argentine.

Cultivation seems to have continued unnoticed by the outside world for many centuries. Finally, in 1897, Spegazzini visited the small Indian village of Amblayo in the mountains of Salta province and was "presented with some excellent little cakes which they said were prepared with Inca wheat of the locality." He took home some of the yellowish seeds and planted them; they grew into amaranth plants different from any known species, which he named *A. edulis* (Spegazzini, 1917, p. 163). Since then *A. edulis* and the Andean *A. caudatus*, both often grown together, have been found repeatedly as grain crops in the four northwestern provinces of the Argentine: Jujuy, Salta, Tucumán, and Catamarca (see fig. 3). Hunziker (1943b, pp. 325–339) gives a detailed summary of previous Argentinian records together with much new information from his own collections. The plants are usually called *quinoa* or *chaclión*, but the Andean name *coimi* is also used in the Argentine province of Jujuy.

The plants are cultivated only in small quantities, often in the maize fields, and it has become rare to find even a few plants; "there is no doubt that the days of *A. edulis* are numbered and that in a little while longer its cultivation will have fallen into oblivion" (Hunziker, 1943b, pp. 328–329).

ASIA

Ancient History.—In later sections of this paper, we shall see that the Asiatic and American grain amaranths are very closely related and that there is reason to believe that the entire group must have been originally domesticated in America. The question of how long they have been grown in the Orient is therefore of considerable interest.

The crop is scattered so widely through Asia and is so firmly entrenched among remote peoples that it gives a powerful impression of great antiquity in the area. Many investigators, from De Candolle (1883, p. 357) and Hooker (1885, p. 718) down to Ames (1939, p. 39), Vavilov (Darlington and Janaki-Ammal, 1945, p. 14), and Merrill (1950, pp. 16–17), have concluded that the crop has certainly been cultivated in southern Asia from time immemorial and probably originated there.

Unfortunately, there is little direct evidence available on the early story of grain amaranths in this area, and it seems unlikely that there will ever be much more. The crop may always have been concentrated, as it is today, in inaccessible highlands, mostly unknown territory to the ancient Oriental writers and early European travellers. The best hope of finding early records would seem to be in India, where the crop is most widespread and important. So far as I know, no one has ever looked in the old Hindu writings for records of these plants.

The ancient Chinese botanical sources have been carefully examined by Bretschneider. It is hardly to be expected that grain amaranths would be recorded in

these sources, since one can search long and vainly for any mention of them in modern botanical literature on China. Only one definite account of the crop in modern China seems to have been published (Hu, 1948). Therefore it is startling to find that Bretschneider (1896, p. 405) presents what seems to be a clear reference to a grain amaranth in an ancient Chinese materia medica. This work, written about 950 A. D. for the Prince of Shu, modern Szechwan, lists six kinds of *hien*, a generic name for a group of related plants, mostly indigenous amaranths cultivated as pot-herbs. Among these were two whose seeds were used in medicine; one was called *jen* (man) *hien*, possibly because it grew tall and erect. We shall see that there is a modern record of grain amaranths from the same area which gives the same name.

Recent.—Since early in the 18th century the grain amaranth species have been collected repeatedly in many parts of Asia (Martyn, 1728, p. 6; Linnaeus, 1763, p. 1406; Miller, 1768, p. 17; Willdenow, 1798, pp. 29–37; and many later sources). However, since these species have become widespread as cultivated ornamentals and occasionally as pot-herbs, their presence does not necessarily indicate cultivation for grain. Many of the collectors noted simply that the plants were cultivated, and there is no way of knowing whether they had found a few ornamentals in an Englishman's flower garden or the staple food crop of the entire region. Such cryptic records are of little value for our present purposes, although they suggest that the grain crop may be grown much more widely than the more definite records prove.

The first European to take an interest in the Asiatic amaranths as a grain crop seems to have been Francis Buchanan-Hamilton. In the early 19th century he found the crop in two widely separated parts of India, the far south and the fringes of the Himalaya.

South India and Ceylon—Buchanan-Hamilton named the white-seeded south Indian grain amaranth *A. frumentaceus*. He discovered it "on the hills between the Mysore and Coimbatore countries, where the natives call it *kiery* and cultivate it for the seed, which they convert into flour and which forms a great part of their subsistence" (Roxburgh, 1832, p. 609). Later Wight (1843, p. 720) wrote of *A. frumentaceus:* "In Coimbatore, Salem, and Madura I have frequently met with large fields of it, often on very steep slopes. The seed ground into meal forms the principal food of the wild inhabitants of these hills." Sykes (1838, p. 241) may have been referring to the same plant and the same area when he listed, among the crops of the Deccan, an amaranth called *rajgeerah* whose seeds were harvested in December and eaten unmilled.

The crop has persisted in these hills into the present century. In 1912 the U. S. Department of Agriculture received seeds of a grain amaranth from the Mysore area (Safford, 1917, p. 297). Finally, Fisher (1921, p. 147) reported that on the Anaimalai Hills at elevations of 2,000 to 4,000 feet the hillmen cultivated a grain amaranth called *kira*.

There are vague reports, with no details given, of cultivation of amaranths in Ceylon for the grain, locally called *landesi* (Hooker, 1885, p. 718; Church, 1886, p. 107; Trimen, 1895, p. 396).

North India—Buchanan-Hamilton gave the name *Amaranthus Anardana* to the white-seeded plants he found cultivated in the fields of Nepal, Bhagalpore, and Cosala, modern Oudh (Wallich, 1828, No. 6903; Madden, 1858, p. 118; Haines, 1922, p. 1247). In his notes he also mentioned that one of the chief crops high in the hills of Kullu was a plant called *chuyá*, which he had not seen but believed to be a grain sorghum (Madden, 1858, p. 118). Madden believed that *chuyá* and *anardana* were one and the same thing, and that *anardana* was an incorrect rendering of *amardana*, as Buchanan-Hamilton once wrote it, meaning immortal grain. He had seen this tall crimson or yellow amaranth cultivated "all over the Himalaya" under various local names, including *ramdana*, grain of the god Rama. The names given this crop in different regions of the Himalaya are bewilderingly variable and will not be catalogued here; many, such as *báthu* and *sag*, are generic terms applied not only to grain amaranths but also to chenopods and the various indigenous amaranths used as pot-herbs.

Later records show that grain amaranths are scattered widely across northern India and the neighboring states. Occasionally they are grown in the plains regions as an irrigated crop during the dry winter monsoon (Watt, 1908, p. 63; Bamber, 1916, p. 314). Little precise information is available on distribution of the crop in the lowlands. Kashyap (1936, p. 205) reports them around Lahore in the Punjab. White-seeded specimens of species commonly grown for grain have been reported in cultivation at Manbhum, Singbhum, and Sambalpur (Haines, 1922, pp. 761–762), but the purpose for which they were grown was not stated. In these plains areas the crop seems to be grown only on a very small scale along field borders, and the grain has a minor use as one of the foods permitted Hindus on their fast days.

Behind the plains, in the foothills and mountains of the Himalaya system, amaranths become an important field crop and a conspicuous feature of the landscape. They have been recorded repeatedly along the whole length of the Himalaya from Kashmir to Bhutan. Important early collections of grain amaranth species were made in Baltistan, Hazara, Kashmir, and Ladak by the Schlagintweit Tibetan expedition of 1856. The available herbarium specimens bear no data on uses, but Thellung reported that one of their collections, at least, was known to come from plants cultivated for the seeds, which were ground into meal (1914, p. 243). Subsequently, cultivation of amaranths as grain crops has been reported in Kashmir, Chamba, Sirmur, especially around Simla, in Bashahr, Tehri, Garhwal, Kumaon, specifically in the Bhotiya and Almora regions, in the mountain tracts of Oudh and Bengal, and in Sikkim (Powell, 1868, p. 244; Watt, 1885, pp. 210–211; Church, 1886, p. 107; Duthie, 1893, p. 24; Lawrence, 1895, p. 338; Gammie, 1898, p. 184; Collett, 1902, p. 411; Bamber, 1916, p. 314; Pant, 1935, p. 46; 83; Millen, letter). Watt also reported the crop in the hills of Burma (1908,

Fig. 4. Asia: Localities and regions where grain amaranth cultivation is indicated.

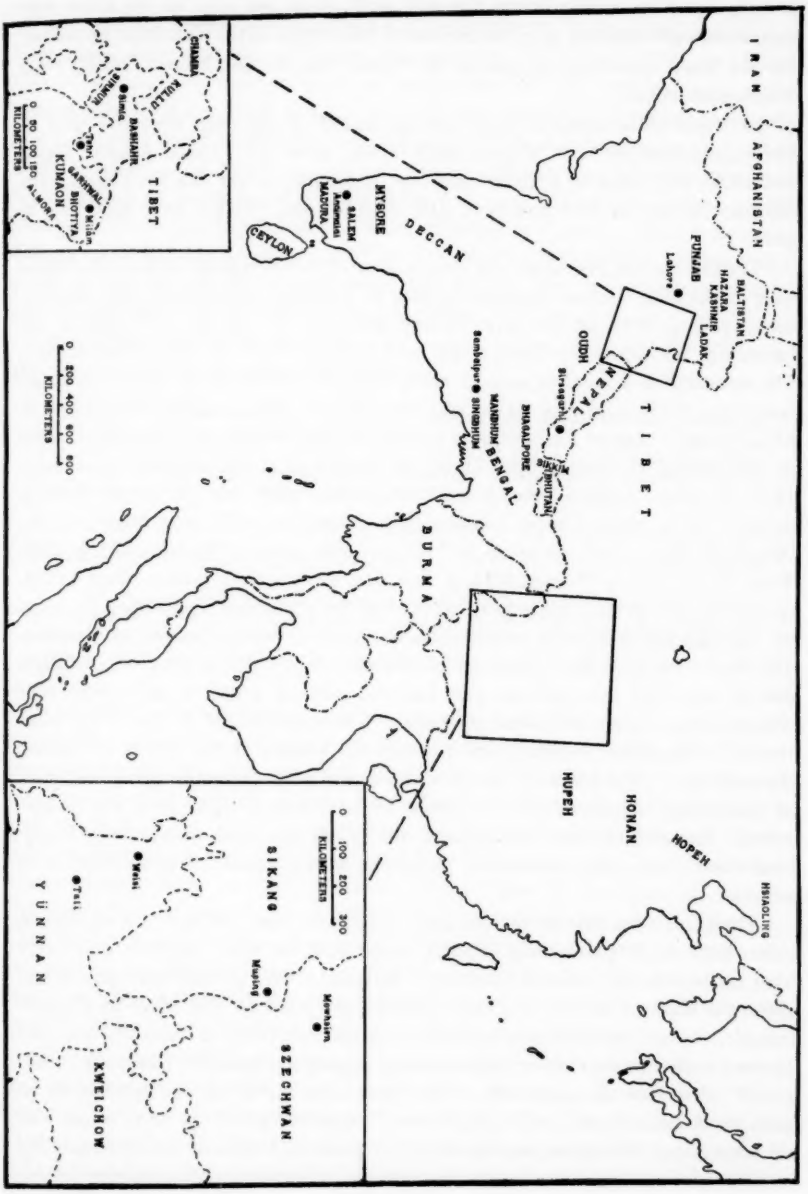

Fig. 4. Asia: Localities and regions where grain amaranth cultivation is indicated.

p. 63), but Stonor, who knows the area well, wrote me that he has never seen amaranths cultivated for grain in the Burma hills or the outer Himalayas of Assam. He has heard that they are grown as a grain crop on the Bhutan border by a Tibetanized tribe.

In Nepal there seems to have been no record of the crop since the time of Buchanan-Hamilton and Wallich until 1948, when Dr. Janaki-Ammal found amaranths cultivated as a grain crop near Sirsagarhi in the Marku Valley. She obtained samples of both pale- and dark-seeded kinds, which I have been able to grow.

Throughout the Himalaya, the crop is planted in unirrigated land at the beginning of the rainy summer monsoon in May or June and is harvested from September on (Watt, 1885, pp. 211–212; Church, 1886, p. 107; Duthie, 1893, pp. 23–24; Lawrence, 1895, p. 338; Watt, 1908, p. 63; Pant, 1935, p. 84; Millen, letter). The amaranth is a favorite crop in newly burned and cleared jungle, as it is not easily injured by wild pigs, bears, and deer (Watt, 1885, p. 211; Pant, 1935, p. 83). In the Valley of Kashmir, it is a relatively minor crop, as in the plains, sown in rows among the cotton fields or on the borders of the maize plots (Lawrence, 1895, p. 338). Around Tehri it is grown in little plots near the houses (Millen, letter). It is planted more extensively as a regular field crop higher in the Himalaya, often at elevations up to 2500 or 3000 meters (Hooker, 1885, p. 718; Watt, 1885, p. 211; Church, 1886, p. 107; also many later writers). Pant (1935, pp. 40–46, 84) gives a fascinating account of the precarious agriculture practiced by the Mongoloid nomads around Milam on the Tibetan frontier of Kumaon. The area is too high for permanent habitation. It is covered with six to twelve feet of snow for over half the year and the growing season is only about four months long. Crops are raised by primitive hoe cultivation in tiny steep plots studded with glacial boulders; the boulders aid growth of the plants by storing the sun's heat. The crops are always stunted, and often ruined by persistent mists or avalanches; sometimes they are buried by early snows before they can be harvested. In spite of these tribulations, the people sow and usually reap barley, buckwheat, and grain amaranths, sometimes at elevations of more than 3500 meters.

The Himalayan plants, like the Latin American ones, are rich and variable in color; their striking coloration is partly responsible for what little attention they have received in the available literature. Madden (1858, p. 118) was enthusiastic about the brilliant crimson and rich yellow of the plants: "The effect of a mountainside, terrace above terrace, covered with distinct fields of these colours, and glowing under the rays of the afternoon sun, is gorgeous indeed." Lawrence (1895, p. 338) described the amaranth as "the most beautiful of all the crops, with its gold, coral, and crimson stalks and flowers." Gammie (1898, p. 184) wrote that the amaranth, "with its ample red and yellow panicles, brightens the landscape, and its fields of vivid hue serve to mark the positions of widely scattered hamlets among the valleys, miles away from the traveller's standpoint."

Many of the writers give more space to the esthetics than to the uses of the crop, particularly since the grain does not enter into commerce. "Visitors to the hills of India are inclined to smile at people who live very largely upon these minute seeds" (Watt, 1908, p. 63). Around Tehri the grain is popped and made into a dough which is patted between the palms of the hands to make thin cakes (Millen, letter). In Nepal the grain is roasted and eaten as balls like popcorn, held together by sugar syrup (Janaki-Ammal, letter). There are a few reports that the seeds are parched, ground to flour, and eaten as a gruel with milk or water (Watt, 1885, p. 210; Lawrence, 1895, p. 338; Pant, 1935, p. 46). Beyond that there are only such general statements as: this grain is "one of the most important sources of food to the hill tribes of India" (Watt, 1885, p. 211).

Afghanistan and Persia—Referring to western Afghanistan and the Khorasan area of Persia, Atkinson (1891, p. 10) wrote:

> "The amaranth, *taj-kharus*, occurs only as a cultivated plant, usually seen thinly scattered through melon and tobacco fields, both the red and yellow flowered varieties. I never met with what I should consider a regular crop of the plant, but it occurred through fields rather as if the natives held, in superstitious veneration, the necessity of growing a few of these plants sparsely spread through their fields. The seed is eaten cooked."

China and Manchuria—Shiu-ying Hu (1948, pp. 32–34) wrote that an amaranth is cultivated in western China:

> ". . . . . as a supplementary crop in corn or cotton fields to fill in the spaces where young plants may have been destroyed by insects or along the margin of the field. The plant often grows to a man's height and is thus called manly *shien*. The crop is harvested when the leaves on the lower two thirds of the stem turn yellow. After the plants are gathered and dried in the sun, they are threshed."

The seeds are known as *tien-shu-tze*, or millet from heaven; they are popped and mixed with a hot sugar syrup made from fermented rice or millet grain. When the mixture cools, it is "cut into thin slices. This candy is crisp, puffy, sweet and well flavored. On the Chinese New Year's Eve, in every farm-house quantities of such candy are made." The Chinese characters on Miss Hu's illustration of manly *shien* are identical to those given for man *hien* in Szechwan in the 10th century (Bretschneider, 1896, p. 405). Miss Hu did not specify the parts of western China in which the crop is grown, but she suggested that I write M. C. Chang at Chengtu for definite information. Chang informed me that grain amaranths are not grown near Chengtu but in far-off mountain areas. He sent me samples of light- and dark-seeded *tien-shu-tze*, grown at elevations of 2000 or 2500 meters near Mowhsien in northwestern Szechwan and Muping in Sikang.

The crop is probably also present to the southwest of Szechwan in Yünnan; amaranths are reported extensively cultivated on the upper Mekong above Weisi and also around Tali (Handel-Mazzetti, 1929, 7:162). The fields are said to "appear generally red" from these plants. Although no mention of use is made, it is hard to imagine such large-scale cultivation as anything but a grain crop. It is conceivable that the crop may extend almost continuously through these poorly known parts of interior Asia from Szechwan to the Himalaya.

On the other side of Szechwan, the trail is not much clearer. Pale-seeded forms of species ordinarily grown for grain have been collected in cultivation in Kweichow and Hupeh, but with no data on use. Small-scale cultivation of amaranths for their edible seeds has been noted in Honan and Hopeh (Hsien-wu, 1935, p. 11; Beach, letter), but no details are available.

These indistinct traces of the crop, extending across so much of the interior of China, finally come to an end in Manchuria. A pale-seeded cultivated amaranth belonging to a grain species was collected in the Hsiaoling area of southern Manchuria by Dorsett in 1925. In northern Manchuria there is a definite account of grain amaranth cultivation (Skvortzow, 1926, p. 15). The crop "is planted in fields by the Chinese for the sake of its small yellow or reddish seeds, which are used in the preparation of little cakes."

AFRICA

Baker and Clarke (1909, p. 32) claim that amaranths are "cultivated throughout warm Africa as a grain." This statement may be an exaggeration based partly on simple records of occurrence of grain amaranth species. In Africa, just as in Asia, some of these species have been widely diffused as garden ornamentals; occasionally they are also cultivated as pot-herbs. I am unable to find any confirmation of grain use of the plants in Africa, except for Dalziel's statement that in Sierra Leone an introduced amaranth "is said to be cultivated for the seed as food" (1948, p. 36).

II. Botanical Classification

So far, in tracing the culture history of the grain amaranths, the problem of their botanical classification has been postponed and species identifications given in the literature have been deliberately ignored. The Latin names given the plants by different authors are bewilderingly variable. They include, for the grain amaranths of Arizona: *caudatus, leucospermus, leucocarpus, Powellii,* and *retroflexus;* for those of Mexico: *caudatus, cruentus, hybridus, leucocarpus, leucospermus,* and *paniculatus;* for those of South America: *caudatus, edulis,* and *leucospermus;* for those of Asia: *Anardana, caudatus, celosioides, cruentus, farinaceus, flavus, frumentaceus, hybridus, hypochondriacus, paniculatus, sanguineus, speciosus,* and *strictus;* and for those of Africa: *Alopecurus* and *caudatus.* Conflicting identifications are not confined to older sources but continue in recent literature and current herbarium determinations.

A little investigation of the published descriptions of these many "species" immediately reveals one important fact: all belong to a closely related group, forming a relatively small section of the genus *Amaranthus.* This section, usually called AMARANTHOTYPUS, is distinguished by having monoecious compound inflorescences and 5-merous flowers with circumscissile utricles (Dumortier, 1827, p. 19; Moquin-Tandon, 1849, p. 255; Thellung, 1914, p. 230). Beyond this single fact, very little sense can be made of the classification of the grain amaranths from a study of the literature. The section AMARANTHOTYPUS is outstanding, even in

the genus *Amaranthus*, for its labyrinth of disputed synonymy and controversial taxonomy.

The confusion is mostly traceable to two factors: the wide dispersal of the species and the subtlety of the differences between them. Their wide distribution is not due solely to their spread as grain crops; the grain species and their close relatives include most of the cosmopolitan ornamental and weed amaranths. Since there has been nothing approaching an adequate general treatment of the genus until the present century, the naming of amaranths has been almost entirely in the hands of persons working on local floras. It was inevitable that such widespread species would receive different Latin names in different regions. The result has been a rich heritage of problems in nomenclature.

The second factor responsible for the confused classification has created a much more serious problem than the superfluous names. Species differences within the section are mostly quantitative and often easier to recognize than describe. Most of the earlier species descriptions are excessively brief and waste their few words on characters common to many species or such trivial characters as pigmentation. Before the extreme importance of flower characters was realized, the damage had been done. The species had been described and named, according to the rules, but many were completely unrecognizable from the original descriptions. Since access to many of the type specimens has been difficult or impossible for most botanists, it is small wonder that concepts of the species have become highly variable.

The obvious solution to these difficulties would be monographic treatment, a formidable project which no one has yet attempted. The closest approach was made by Thellung in his treatment of *Amaranthus* for a flora of Europe (1914). Thellung's work is an admirable piece of scholarship, based on careful herbarium study, emphasizing microscopic flower characters, and on exhaustive bibliographic research. Unfortunately, the purpose of the work required Thellung to concentrate his attention on the European flora, which has few native amaranth species. He concluded that all the species of AMARANTHOTYPUS present in Europe are recent immigrants, none of which arrived before the 16th century. The specimens he worked with consisted mostly of adventive weeds and a jumble of cultivated plants, often hybridized and usually of forgotten origin, which had been propagated for generations in European gardens. Considering these fantastic handicaps, Thellung's insight into the group was remarkable. His reduction of over forty "species" of AMARANTHOTYPUS to five and his detailed descriptions of the entities, often based on re-examination of Linnaean types, represent great forward steps.

There have been two important taxonomic works involving this group since Thellung's work. Standley's treatment of the genus for the 'North American Flora' (1917) is particularly useful for the North American endemic species; his systematic treatment of the section AMARANTHOTYPUS is little more than a simplification and modification of Thellung's treatment. Hunziker's morphological investigation of the grain amaranths (1943b), is also of considerable value, particularly for the South American crop plants, on which most of his work was done.

The best hope for fuller understanding and more convincing classification would seem to lie in a study of the entire section throughout its range. A start on this ambitious project is attempted here.

METHOD OF INVESTIGATION

The procedure adopted was to put aside all the conflicting identifications, both in published literature and on herbarium sheets, and make a fresh start by re-examining individual specimens. Specimens of the cultivated grain amaranths were mostly obtained by growing seed collections from many different sources in the New and Old World. Half a dozen to a dozen plants were grown from each seed sample in various greenhouse and outdoor plantings, both in Missouri and in California. I was able to make some field collections of non-cultivated amaranths in the United States, Mexico, and Guatemala. However, most of the wild and weed amaranths examined, as well as a few of the grain amaranths, were obtained from the collections of four herbaria: the U. S. National Herbarium, the Gray Herbarium, the University of California Herbarium, and the Herbarium of the Missouri Botanical Garden. Material examined from these institutions included their complete collections of the section AMARANTHOTYPUS from Latin America, Asia, and Africa, and a sampling of their collections from the United States. The specimens examined are listed on pages 620–623. A limited amount of material from Europe was examined, but is not included in the presentation, since the grain species and their close relatives are present in Europe only as recent immigrants.

I had originally hoped that chromosome counts might be of some help in classification. The few published counts indicate that there are two groups of species in the section AMARANTHOTYPUS, one with a diploid chromosome number of 32, the other with 34 (Takagi, 1933, p. 556; Murray, 1938, p. 317). I prepared root-tip sections of several species and obtained counts in the low 30's for all of them. In my preparations it was very difficult to obtain precise counts; the apparent number of chromosomes varied considerably between different cells of a single section. I suspect that other persons have had the same difficulty. For example, Takagi reported a diploid number of 32 for *A. caudatus;* in 1948 Dr. Cárdenas wrote me that he had found the diploid number in both *A. caudatus* and its wild relatives in Bolivia to be 32, but in a later publication (Cárdenas, 1949, p. 114) he reported counts of 34 for these same species. I am not convinced that the reported variations in chromosome number actually exist. In any case, the numbers are too difficult to determine in this group to be of much use in classification. It seemed best to rely entirely on morphological characters, at least in this preliminary attempt at classification.

Major attention was given to the morphology of the flowers, which were examined under a low-power dissecting microscope. There is always much variation between flowers on an individual plant, so that characterization by examination of one or a few flowers is unsafe. When a sufficiently large number of flowers is examined, a single reasonably constant type can be distinguished, which appears over and over again among the many other inconstant and non-repeating variants.

The abundance of flowers on an individual amaranth is one of the few consolations in studying this generally unattractive plant.

Mature flowers of each specimen were scored for about two dozen different items, involving number, size, and shape of all parts. Exact scale drawings were made of all specimens that appeared even slightly different from ones previously drawn. By means of such sketches several characters which have not received much previous attention are seen to be of distinct diagnostic value (see figs. 5 and 6).

An attempt was made to score macroscopic characters, particularly configuration of the inflorescence, but these proved to be of little value in classification. Such characters are difficult to measure or express objectively and are extremely dependent on the age of the plant and on environmental variables.

When examination and scoring were completed, it was found that the great majority of the available specimens could readily be sorted, on the basis of flower characters alone, into a few reasonably homogeneous groups. It then became evident that the vague and largely subjectively appreciable differences in vegetative characters and inflorescence aspect fitted these groupings quite well.

Finally, an attempt was made to determine the correct names for the major entities recognized; no attempt was made to give Latin names to the lesser entities. Where type specimens are not available, I have tried to do the least possible violence to existing species concepts, particularly those of Thellung and Standley. Standley's numerous herbarium determinations are outstanding for their consistency among the ruck of carelessly given names.

The following sections outline the distributions and the more distinctive characteristics of the entities recognized. Unless otherwise stated, the geographic distributions are based entirely on specimens examined. The grain species are considered first, followed by the closely related wild and weed species.

GRAIN SPECIES

The cultivated grain amaranth species are so very much alike, not only in appearance but in many technical characters, that the prevailing confusion is not at all surprising. All are coarse annual herbs with similar leaves and branching habit, erect and tall, sometimes growing higher than a man. The obvious plant and seed color differences, which have been used as varietal or even specific characters by too many botanists, are of little taxonomic value. *Amaranthus edulis* plants apparently always lack red pigment and are always pale-seeded, but each of the other three species has dark- and pale-seeded forms, and in plant color each varies from deep red to bright green. These color characters seem to be freely exchanged within an otherwise homogeneous population and are commonly highly variable in a single seed lot.

All the grain amaranths characteristically have great compound inflorescences, terminal on the main stem and side branches. The basic units of the inflorescence are little dichasial cymes, usually called glomerules, each ordinarily consisting of an initial staminate flower and an indefinite number of pistillate flowers. The

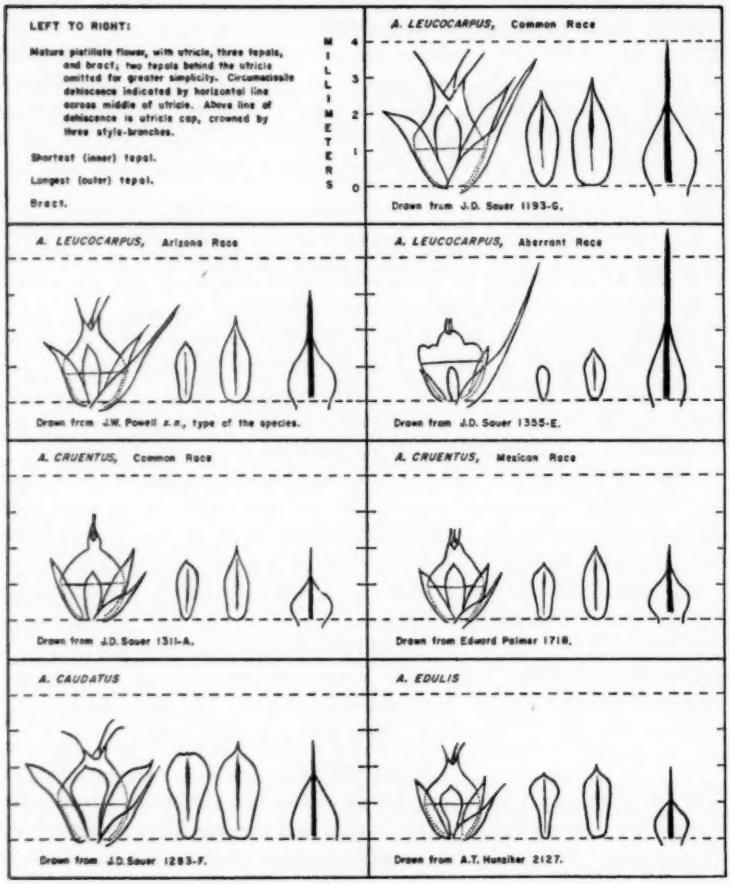
LEFT TO RIGHT:
Mature pistillate flower, with utricle, three tepals, and bract; two tepals behind the utricle omitted for greater simplicity. Circumscissile dehiscence indicated by horizontal line across middle of utricle. Above line of dehiscence is utricle cap, crowned by three style-branches.
Shortest (inner) tepal.
Longest (outer) tepal.
Bract.
MILLIMETERS
4
3
2
1
0
A. LEUCOCARPUS, Common Race
Drawn from J.D. Sauer 1193-G.
A. LEUCOCARPUS, Arizona Race
Drawn from J.W. Powell s.n., type of the species.
A. LEUCOCARPUS, Aberrant Race
Drawn from J.D. Sauer 1355-E.
A. CRUENTUS, Common Race
Drawn from J.D. Sauer 1311-A.
A. CRUENTUS, Mexican Race
Drawn from Edward Palmer 1718.
A. CAUDATUS
Drawn from J.D. Sauer 1283-F.
A. EDULIS
Drawn from A.T. Hunziker 2127.

Fig. 5. Grain amaranth species. Scale drawings of pistillate flowers.

glomerules are crowded on a leafless axis to form complex inflorescences, technically thyrses, which are generally called spikes. When grown under unfavorable day-length conditions, the plants begin to bloom when only a couple of inches high and manage to produce only a simple small terminal spike. When grown under proper day-length conditions, all of the grain species are capable of putting forth a huge inflorescence, with a large terminal spike and fifty or a hundred lateral spikes, which may themselves bear branch spikes.

In all the grain species each flower is subtended by a sharp-pointed bract (fig. 5); the perianth consists of five free tepals; the male flowers characteristically have

five stamens, the female a single circumscissile utricle. Within this common framework, the following entities can be recognized.

Amaranthus leucocarpus S. Wats.—

This species was originally described by Watson (1875, p. 347) on the basis of plants grown from a single seed lot, obtained in Arizona by J. W. Powell. So far as I know, the species has not subsequently been collected in Arizona, but very similar plants have been widely collected elsewhere, particularly in Mexico. As defined here, the species is divided into races, with the type collection of the speciés assigned to the Arizona race. The more common and widespread race differs slightly from Watson's type, but includes Mexican specimens identified as *A. leucocarpus* by Watson himself (1887, p. 446). The species name was poorly chosen, since it was the color of the seeds, rather than the color of the fruit, which attracted Watson's attention. He later (1887, p. 446) attempted to change the name to *A. leucospermus*, but under the rules this later synonym is illegitimate.

In published works, *A. leucocarpus* is commonly reduced to a variety or synonym of either *A. caudatus* L. or *A. hybridus* L. Herbarium specimens of this group are commonly identified as either *A. paniculatus* L. or *A. hypochondriacus* L. There are morphological and geographical arguments against identifying the group which includes Watson's type with any of these Linnaean names. However, it is quite possible that *A. leucocarpus* may eventually prove to be a synonym of some other early name. For example, Wight's illustration (1843, p. 720) of *A. frumentaceus* Buchanan-Hamilton suggests that this poorly known species may be identical to *A. leucocarpus*. In the meantime, it is expedient to retain Watson's epithet, as it is the only one in common use which can definitely be tied to this distinctive group of amaranths.

Common Race of A. leucocarpus.—This race is perhaps more widespread and important as a grain crop than any other amaranth and also includes one of the common ornamental forms, sometimes known as Prince's Feather.

As a grain crop its known distribution includes many places in Mexico: Guasaremos and Rancho Trigo in Chihuahua (see fig. 1), Quebrada de Manzana in Sinaloa, Guadalajara and Tlajomulco in Jalisco, Teremendo and Opopeo in Michoacán, San Gregorio Atlapulco and nearby villages in the Distrito Federal, Amaxac and San Miguel del Milagro in Tlaxcala, Teocuizmanalco in Puebla, Chilapa in Guerrero, and Ixtlán de Juárez in Oaxaca. The specimen from Secanquim in Guatemala, previously mentioned as probably representing a grain crop, also belongs to this race. In Asia the race has been collected in Iran and Afghanistan; in many regions of the Himalaya: Baltistan, Hazora, Kashmir, Ladak, Chamba, Bashahr, Sirmur, Garhwal, Kumaon (labelled *A. Anardana*), Nepal, and Sikkim; in various provinces of China: Sikang, Yünnan, Kweichow, Szechwan, Hupeh, Kiangsu, and Shantung; and in Manchuria. Many of these Asiatic specimens bear the simple notation "cultivated" or "crop" but almost none are accompanied by any information on the purpose for which they are grown. Only the specimens grown from seed collected for me in Nepal by Dr. Janaki-Ammal are positively

identified as a grain crop. However, the distribution pattern of this race in Asia coincides strikingly well with the area of grain amaranth cultivation reported in the literature.

As an ornamental the race is widely grown in Europe and the United States. The only available African specimen is from Morocco and may represent an ornamental brought from Europe.

Outside of cultivation, the race has been collected only as an infrequent escape at widely scattered places in the United States, Mexico, Asia, and Europe.

The mature inflorescences of this race are remarkable among the cultivated amaranths for their stiff appearance (pl. 13A). Both terminal and lateral spikes are usually long and thick and often erect. The bracts are especially large and long-pointed, giving the inflorescence a prickly appearance. The tepals also are longer than in the other grain amaranths, slightly recurved, and usually acute-tipped (fig. 5). The utricle cap is large and slopes gradually to the extremely thick bases of the recurved style-branches, which usually meet in a sharp cleft. The Mexican populations are overwhelmingly pale-seeded, although several have a small proportion of dark-seeded forms mixed in. In the Asiatic collections dark-seeded plants are more numerous but still in the minority. The plants grown as ornamentals in Europe and the United States seem to be invariably dark-seeded.

There is minor but definite variation in flower characters within and between many of the Mexican collections. Some members of the Oaxaca and Guerrero collections show some resemblances to the Mexican race of *A. cruentus*, described below. All of the United States and Old World collections examined are virtually identical in flower characters and are exactly like some of the Mexican plants.

Arizona Race of A. leucocarpus.—This race is known only from the single 19th-century seed collection from some mysterious Arizona Indian tribe. All the available specimens were grown at the botanical garden of Harvard University. The vegetative characters and inflorescence aspect (pl. 13B) of the plants were probably marked by this exotic environment. The less plastic flower characters are very similar to those of the preceding race, except that the parts are all noticeably smaller and the style-branches less thick (fig. 5). The three available specimens are all pale-seeded.

Aberrant Race of A. leucocarpus.—One of the Mexican grain amaranths is quite unlike any recognized species. It seems best not to give it a Latin name until it is more adequately collected and understood. It is placed here provisionally, since it is grown within the range of *A. leucocarpus* and may be nothing more than a cross between it and some other very dissimilar species. This race is known only from Dr. West's collection from Los Reyes in Michoacán, where it is cultivated as a grain crop.

The inflorescences (pl. 13C) are much like those of the common race of *A. leucocarpus*, but the flowers are completely different. The stamen and tepal numbers vary between 4 and 5 in an individual inflorescence. The bracts have a narrow lamina and an extremely long point, while the tepals are greatly reduced in size

and often without visible nerves. The utricle cap is very rugose and flattened and the style-branches are extremely short.

There is only minor variation between the half dozen plants of West's seed collection that I have grown. All are dark-seeded.

Amaranthus cruentus L.—

Linnaeus described this species from Chinese plants (1759, 2:1269). His ambiguous description was clarified by Thellung (1914, p. 243) after re-examination of Linnaeus' material. There can be little doubt that the species under consideration here is the same as Linnaeus' *A. cruentus*. The plants included here which were determined by Standley are consistently labelled *A. cruentus*. Nevertheless, other taxonomists have given this species a variety of other names in herbaria; many of the Asiatic specimens have been labelled *A. paniculatus* L., a name reduced to synonymy with *A. cruentus* by Thellung and Standley.

Common Race of A. cruentus.—This group is known as a grain crop only at three places in Guatemala: San Martín Jilotepeque, San Juan Sacatepéquez, and Cobán. The specimen previously mentioned as collected in a maize field at Cubilquitz, which may have been grown for grain, also belongs here.

As an ornamental the race is cultivated over much of the world and is occasionally collected as an escape at widely-scattered places. Specimens have been examined from a few places in the United States all the way from Massachusetts and South Carolina to California; the states of Puebla, Vera Cruz, and Oaxaca in Mexico; British Honduras, Guatemala, El Salvador, Nicaragua, Panama, Porto Rico, Haiti, the Dominican Republic, Barbados; the departments of Atlantico, Antióquia, Cauca, and Cundinamarca in Colombia; Ecuador; Mérida in Venezuela; the states of Pernambuco, Minas Geraes, and São Paulo in Brazil; Hawaii, the Fiji Islands, New Guinea, Sumatra, British North Borneo; the islands of Mindanao, Mindoro, and Luzon in the Philippines; Japan; the provinces of Kiangsu, Anhwei, and Chekiang in China; Annam in Indo-China; Kenya and Uganda in British East Africa; and Coquilhatville in the Belgian Congo.

The inflorescences of this race are much more lax and usually more slender than those of *A. leucocarpus* (see pl. 13D). Though the slender bract points extend well beyond the laminas, the bracts are very small, so that the inflorescence has a soft appearance. The tepals are characteristically much shorter and slightly less acute than in *A. leucocarpus* and they are not recurved. The utricle cap is unique among all the amaranth species I have seen, being contracted into a narrow tower below the bases of the style-branches; the style-branches are slender and erect.

Except for some variation in tepal length, most noticeable in the Central American specimens, this race is very homogeneous. The Guatemalan grain specimens are both pale- and dark-seeded, in about equal proportions. All the other specimens are dark-seeded.

Mexican Race of A. cruentus.—This group has a curiously scattered distribution in Mexico: Acatlán in Puebla, Zimatlán in Oaxaca, Ymala in Sinaloa, and

Cusihuiriáchic in Chihuahua. It is known to be a cultivated grain crop at all these places except Cusihuiriáchic, where it was collected without data. An amaranth very closely related to this group is cultivated by the Pueblo peoples of the southwestern United States as a dye plant (J. Sauer, in press).

In inflorescence (pl. 14A) and most flower characters this race is very close to the common race of *A. cruentus*. It differs mainly in the shape of the utricle cap, which appears to be intermediate between *A. cruentus* and *A. leucocarpus* or *A. hybridus*. All the grain specimens are pale-seeded; the specimen from Cusihuiriáchic and the Pueblo dye plants are dark-seeded.

Amaranthus caudatus L.—

As mentioned in the discussion of grain amaranth cultivation in South America, this species was originally described from Peru. Thanks to the strikingly long and drooping tail-like inflorescence, which gives the species its name, the species has been more consistently recognized than most of the others. Nevertheless, specimens of *A. caudatus* are often mislabelled in herbaria, and at least one later synonym, *A. Alopecurus*, is found in the literature. The name *A. Alopecurus* was given by Hochstetter to a group of specimens collected in Abyssinia, which he apparently believed represented an endemic African species. All the collections cited in the original description of *A. Alopecurus* (Braun and Bouché, 1872) have been examined and found to be indistinguishable from South American collections of *A. caudatus*.

This is the second of the great grain amaranth species; it is grown as a crop in both South America and the Old World. Specimens known to represent the grain crop are available from several Andean places: La Mejorada, Ollantaytambo, and Cuzco in Peru; Sacaba, Angostura, and Tarija in Bolivia; San Carlos in Argentina. As in the case of *A. leucocarpus*, most of the Old World specimens are marked as cultivated, but almost none are accompanied by any data on the reason for cultivation. Janaki-Ammal found *A. caudatus* grown for grain in Nepal, along with *A. leucocarpus*. The known distribution of the species in Asia is strikingly like that of *A. leucocarpus* and of the localities in published records of grain amaranths. Specimens are available from Afghanistan, Baltistan, Ladak, Kumaon, and Nepal in the Himalaya; Yünnan and Szechwan provinces in China; and Manchuria. The published records of grain amaranth cultivation in Africa identify the plants as *A. caudatus* or *A. Alopecurus*. The species has been collected not only in Abyssinia, where it is apparently ruderal, but also in the Sudan and the Belgian Congo. None of the available specimens bear any data on use of the plants.

The species includes the familiar ornamental Love-lies-bleeding, grown in many parts of the world and infrequently collected as an escape.

The inflorescences are quite distinctive in that they usually have an extremely long, thick, trailing terminal spike. The individual glomerules become quite large and are relatively far apart, giving the spikes a peculiar knobby appearance. The "tail" is most conspicuous in the ornamental forms, which commonly have only a few lateral spikes. Many of the South American grain specimens also have the

long "tail" with few lateral spikes (pl. 14B), but others have an inflorescence more like that of *A. cruentus*, with a relatively inconspicuous terminal spike and many lax lateral spikes.

The bracts are usually fairly short and the laminas have broader bases than in the preceding species. The tepals are very broad toward the tips, often overlapping, and are strongly recurved. Even the outer tepals are somewhat obovate and the inner are definitely spatulate with a narrow claw. The inner tepals are obtuse-tipped or even emarginate. The style-branches are recurved, as in *A. leucocarpus*, but they are usually less thick and meet in a saddle rather than a cleft. The South American grain specimens are predominantly pale-seeded, but there are some reddish-seeded and some dark-seeded plants in most of the collections. The other specimens are mostly reddish-seeded, but a few of the Asiatic and African specimens have dark seeds.

There is much minor variation in flower characters within this species, particularly in the South American collections. One plant collected at San Carlos in Argentina deserves special mention. It is known to be derived from a mixed population of *A. caudatus* and *A. edulis*, grown together as a grain crop. Its inflorescence is approximately like that of other specimens of *A. caudatus*, and it lacks the polymerous staminate flowers which supply the key character of *A. edulis*. However, the pistillate flowers are almost indistinguishable from those of *A. edulis*.

Amaranthus edulis Spegazzini.—

This species was described by Spegazzini (1917, p. 163) from grain amaranths discovered at Amblayo in the Argentine province of Salta. The species has subsequently been found, always as a pale-seeded grain crop, only at a few other places in Salta and the neighboring provinces of Tucumán and Jujuy (Hunziker, 1943b, p. 325). Specimens are available to me only from Cachí, San Carlos, and another unidentified locality in Salta province.

The inflorescence of this species is its most distinctive feature. Instead of the indeterminate thyrse common to the other species of AMARANTHOTYPUS, this species has inflorescence branches terminated by a peculiar 7- to 9-merous staminate flower. The non-terminal staminate flowers have the usual 5 parts. As a result of their determinate growth, the spikes become extraordinarily blunt and club-shaped (pl. 14C). In pistillate flower characters the species is not extremely different from *A. caudatus*. The tepals are smaller and less strongly recurved and the style-branches are erect. A specimen from the mixed population at San Carlos is especially similar to *A. caudatus*.

NON-CULTIVATED SPECIES

Several species belonging to the section AMARANTHOTYPUS are recognizable among the wild and weed specimens examined. These share with the grain species the characters of the section: monoecious compound terminal inflorescences, 5-merous flowers, and circumscissile fruits. The non-cultivated plants are characteristically much smaller than the grain plants and have smaller flowers and

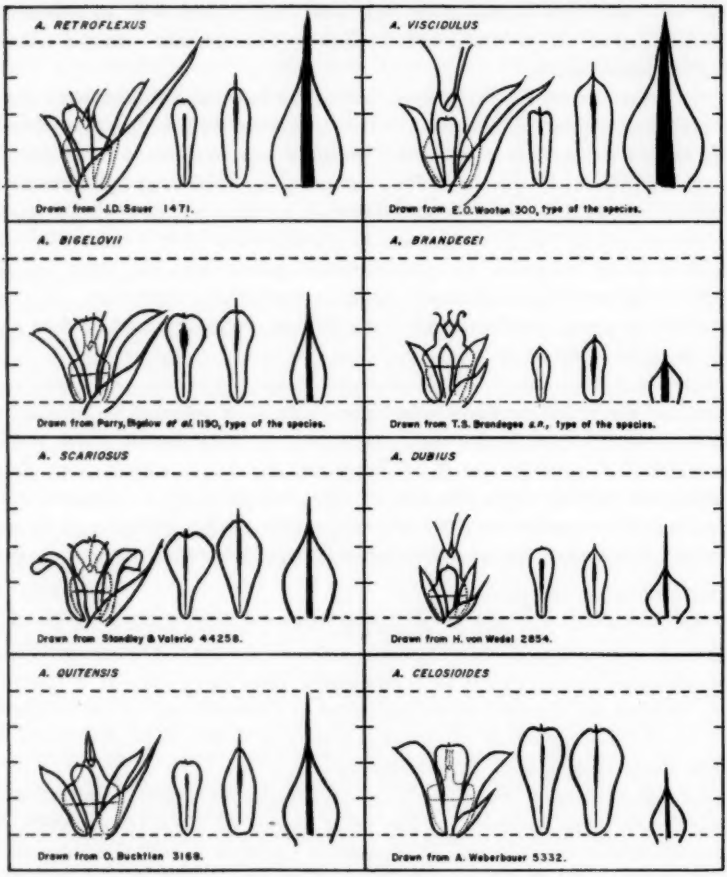
A. RETROFLEXUS
Drawn from J.D. Sauer 1471.
A. VISCIDULUS
Drawn from E.O. Wooton 300, type of the species.
A. BIGELOVII
Drawn from Parry, Bigelow et al. 1190, type of the species.
A. BRANDEGEI
Drawn from T.S. Brandegee s.n., type of the species.
A. SCARIOSUS
Drawn from Standley & Valerio 44258.
A. DUBIUS
Drawn from H. von Wedel 2854.
A. QUITENSIS
Drawn from O. Buchtien 3168.
A. CELOSIOIDES
Drawn from A. Weberbauer 5332.

Fig. 6. Non-cultivated species of section AMARANTHOTYPUS. Scale drawings of pistillate flowers. (For explanation see fig. 5.)

fruits (fig. 6). They are invariably dark-seeded.

A distinction between weed species and truly wild species would be most desirable, but is not feasible since few of the available herbarium specimens bear adequate habitat data. Moreover, even in a field study such a distinction would be very difficult; throughout most of Latin America today, amaranths and other plants eaten by the ever-present livestock are difficult to find in natural habitats. Even the species which are not particularly weedy could be expected to be most abundant where they are protected by walls and fences.

The non-cultivated species are here arranged, as were the grain species, in rough geographic sequence from north to south, as they occur in the New World. Two

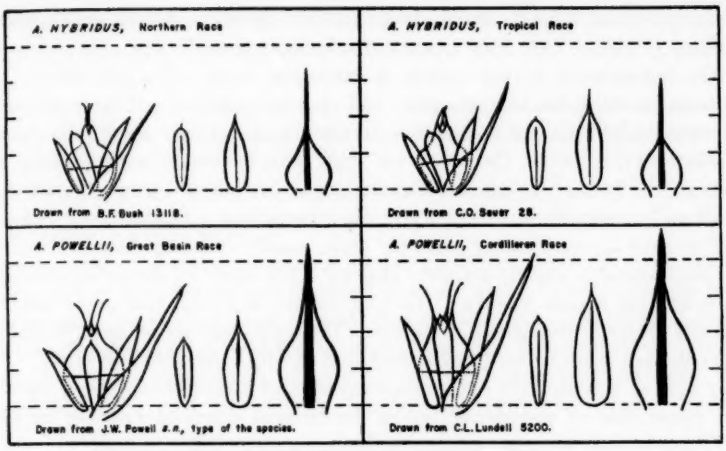
A. HYBRIDUS, Northern Race
Drawn from B.F. Bush 13118.
A. HYBRIDUS, Tropical Race
Drawn from C.O. Sauer 28.
A. POWELLII, Great Basin Race
Drawn from J.W. Powell s.n., type of the species.
A. POWELLII, Cordilleran Race
Drawn from C.L. Lundell 5200.

Fig. 6. Continued.

species, *A. hybridus* and *A. Powellii*, with a wide latitudinal range will be considered last. Another species, *A. spinosus*, which is usually included in this section of the genus, is not discussed here; it is a widespread tropical weed quite similar in many ways to *A. dubius* (see below), but not very similar to any of the grain species. It is readily distinguished from all the other species of the section not only by the peculiar spines but also by the anomalous arrangement of staminate and pistillate flowers in the inflorescence. The peculiar distribution of sexes in the inflorescence of *A. spinosus* is discussed in detail by Murray (1940a).

Amaranthus retroflexus L.—

Linnaeus gave the home of this species as Pennsylvania (1753, 2:991); his specimens were grown in pots from seeds collected by Peter Kalm. The name was suggested by a "deformed example with backward-bent branches" (Thellung, 1914, p. 254). The original description was ambiguous, but has been amplified by Thellung and others. There is fairly good agreement as to the nature of the species, both in the literature and in herbarium determinations, although confusion with other species, particularly *A. hybridus*, is by no means unusual.

This is one of the most abundant and widespread of the North American weed amaranths. It has been collected, almost invariably in disturbed habitats, over most of the United States and at scattered places elsewhere. Specimens are available from: Ontario, New Hampshire, Massachusetts, Connecticut, New York, New Jersey, Pennsylvania, the District of Columbia, West Virginia, South Carolina, Florida, Louisiana, Michigan, Indiana, Illinois, Minnesota, Iowa, Missouri; North and South Dakota, Nebraska, Kansas, Oklahoma, Texas, Montana, Colorado, New Mexico, Arizona, Idaho, Utah, Oregon, and California; also from Coahuila, Mexico; from Japan; from Hopeh and Shantung provinces in China; Kashmir in India;

Uzbekistan in the U.S.S.R.; Persia, Iraq, Armenia, Palestine, Algeria and Morocco. Thellung (1914, p. 254) cites numerous collections from Europe.

The inflorescence of this species is extremely thick, stiff, and erect. The numerous lateral spikes are quite short and crowded together. (One small group of specimens from Coahuila, Mexico, is distinctive in having a small inflorescence without lateral spikes.) The bracts are large, with unusually heavy midribs; the points of the bracts, though not long-excurrent beyond the laminas, commonly extend well beyond the flowers and give the inflorescence a rough, bristly look.

The tepals are much longer than the fruit, usually definitely recurved near the tips, and obovate or slightly spatulate (fig. 6). The tepals are somewhat indurated at the bases in mature flowers. The inner tepals, and often the outer also, are definitely obtuse or emarginate at the tips. The style-branches are erect or slightly recurved; their bases are moderately thick and usually form a shallow cleft.

It may be possible with refined measurements of flower characters to separate some minor races of this species, but in the material examined variation between individuals scarcely exceeds variation within some single inflorescences.

Amaranthus viscidulus Greene.—

This species was described by Greene (1898, p. 344) from a specimen collected in the Sierra Blanca south of Carrizozo, New Mexico. It has since been collected only in the same mountains and a little to the north, near Pecos. Standley considered *A. viscidulus* as a synonym of *A. bracteosus* (1914, p. 508), but comparison of the type specimens shows little similarity in flower characters. Among other differences, *A. viscidulus* is uniformly 5-merous, while *A. bracteosus* has a reduced stamen number. *A. bracteosus* is here considered a synonym of *A. Powellii* (see below).

This species has a small unbranched terminal inflorescence, with a very prickly aspect because of the large bracts. The bracts and tepals are much like those of *A. retroflexus*, but the tepals are more strongly recurved and more extremely emarginate. The utricle cap has a distinctive large tower below the style-branches, which are unusually long.

Amaranthus Bigelovii Uline & Bray.—

This is another minor endemic species, described from western Texas by Uline and Bray (1894, p. 271). I have seen only the type specimen. As in *A. viscidulus*, there is only a small unbranched terminal inflorescence. The bracts are moderately large, with a narrow midrib. The tepals extend well beyond the small fruit; they are strongly recurved, definitely spatulate and emarginate, and somewhat indurated at the bases. The style-branches are erect and of medium length; their bases are slender and form a shallow cleft.

Amaranthus Brandegei Standley.—

This is another minor endemic species, described by Standley (1917, p. 109) from a plant collected in Sinaloa, Mexico. I have seen only the type and another specimen from Colima.

The individual cymes of the inflorescence are predominantly monochasial rather than dichasial; as a result the entire inflorescence has a lax, spindly aspect. The bracts are short, with a heavy midrib which does not extend far beyond the lamina. The tepals are about as long as the fruit, acute-tipped, definitely recurved, and heavily thickened at the base. The style-branches are very short and have especially thick bases.

The stamen number is uniformly 5, not 2–3 as stated in the original description.

Amaranthus scariosus Benth.—

The original description of this species (Bentham, 1844, p. 158) was accompanied by good drawings of the flowers, which leave no doubt as to the species characters. The type specimen was collected on Isla Tigre in the Gulf of Fonseca off the Honduras coast. Specimens have since been collected in the states of Guerrero, Vera Cruz, and Yucatan in Mexico, in Guatemala, El Salvador, Honduras, Nicaragua, and Costa Rica. The few specimens with habitat data were weeds of disturbed sites.

The terminal and lateral spikes of the inflorescence are moderately thick, very long, and erect. The entire inflorescence is large and showy, so that the plants look much more like cultigens than any of the other weed species. Except for its totally different inflorescence, the species is similar to *A. Bigelovii*. The bracts are fairly long, with a slender midrib extending into a moderately long point. The strongly recurved tepals extend well beyond the small fruit; in the mature flowers they become heavily indurated at their bases. The outer tepals are obovate and acutish at the tips, the inner definitely spatulate and emarginate. The utricle cap is extremely rugose above the line of dehiscence. The style-branches are of médium length and slightly recurved; their bases are slender and meet in a shallow cleft.

Amaranthus dubius Mart. ex Thellung.—

For a long time this species was erroneously given the Linnaean name *A. tristis* (Willdenow, 1798, p. 21; Moquin-Tandon, 1849, p. 260; etc.). Thellung's investigation of Linnaeus' specimens showed that the name *A. tristis* was originally applied to an entirely different entity (Thellung, 1912, p. 203; 1914, p. 265), and that there was no valid name available for this species. Thellung gave a full description of the species under the name *A. dubius*, previously published only as a *nomen nudum* by Martius (1814, p. 197). The name *A. dubius* has since been generally adopted for this species in herbarium determinations and published floras.

Amaranthus dubius is the common weed amaranth of the Caribbean; specimens are available from Cuba, Grand Cayman, Jamaica, Haiti, the Dominican Republic, Porto Rico, St. Croix, St. Thomas, Grenada, Trinidad, and Curaçao. On the mainland it has been found in the states of Campeche and Yucatan in Mexico; in Guatemala; Costa Rica; Panama; the departments of Antióquia, Santa Marta, Valle del Cauca, and Bolivar, in Colombia; Nueva Esparta in Venezuela; British Guiana; and in Surinam. Only a few collections are available from outside this area: one from a boat landing in Massachusetts, one from the port of Mazatlán on the west coast of Mexico, and a few from Hawaii and the Marshall Islands.

The spikes are quite variable in number and length; they are relatively slender and quite lax and soft-looking. The bracts are small, seldom exceeding the flowers; their midribs are slender and extend beyond the laminas in points. The tepals are about the same length as the mature fruits, incurved rather than recurved, and not indurated at the base. The outer tepals are oblong and acute-tipped, the inner obovate and obtuse-tipped. The small utricles have a relatively large tower below the style-branches, which are usually erect and long.

Amaranthus quitensis H.B.K.—

This species was described by Kunth (1817, p. 194) from plants collected in Ecuador. The original description is ambiguous and I have been unable to borrow the type material. The interpretation of the species here is based on the detailed description by Thellung (1914, p. 252), who had access to the Humboldt and Bonpland collection. About half of the specimens here included were labelled *A. quitensis* on the herbarium sheets; the others were given a wide variety of names.

This species is one of the most widespread weed amaranths of South America. It has been collected in the provinces of Buenos Aires, Córdoba, Formosa, Santiago del Estero, Tucumán, Salta, Jujuy, and Misiones in Argentina; in La Paz in Bolivia; in Ecuador; and in the Galapagos Islands.

The mature inflorescences are comparatively large, with many long lax lateral spikes. The bracts are long, with a moderately heavy midrib and moderately long point. The tepals are longer than the mature fruits and definitely recurved. The outer tepals are oblong or slightly obovate, and acute-tipped; the inner are obovate or broadly spatulate, and obtuse-tipped. The style-branches are usually erect and fairly long; their bases are rather slender and meet in a shallow cleft.

Amaranthus celosioides H.B.K.—

This is another species rather ambiguously described by Kunth (1817, p. 194), for which the type material is not available. The type collection was made in Venezuela. I have seen no Venezuelan material which agrees with the description of this species, but four specimens are available from Peru and Ecuador which can be tentatively assigned here. All of these were determined as *A. celosioides* by Standley and two were cited by him in a published flora of Peru (1937, p. 484).

All these specimens have the peculiar small bracts with very short points, used by Thellung (1914, p. 251) as the key character of the species. They also share a peculiar utricle cap, contracted into a narrow tower below the erect style-branches. In other characters the available specimens are extremely variable and some may be of hybrid origin. Additional collections and re-examination of the type are badly needed for better definition of this species.

Amaranthus hybridus L.—

Up to this point, few obvious intermediates between species have been encountered and definition of the species has been reasonably simple. Any hybridization which may occur between the species considered so far must be too infrequent to obscure the entities.

Nevertheless, the amaranths are notorious for their ability to hybridize. Accidental interspecific hybrids in great variety have been reported by many writers, from Willdenow (1798) and Regel (1849) to Thellung (1914, 1928) and Priszter (1949); various artificial crosses have been made by Murray (1938, 1940a, 1940b). Most of the accidental hybrids have been found in Europe, where species native to many different parts of the world have come into contact as weeds or been brought together in botanical gardens. In the regions under consideration here, few species have overlapping ranges, and the possible hybrid combinations are very limited. However, there is one species of section AMARANTHOTYPUS, *A. hybridus*, which has an especially wide range, overlapping that of various other species. Here, for the first time, we encounter variants which approach other species and cause serious difficulty in definition of the entity.

In the original description of *A. hybridus*, Linnaeus gave its home as Virginia (1753, 2:990), citing also Ray's earlier report of the plants as wild in New England. Linnaeus' species *A. hypochondriacus*, also attributed to Virginia and New England (1753, 2:991), was distinguished from *A. hybridus* only by having reddish rather than green pigmentation; it is generally regarded as synonymous with *A. hybridus* (Thellung, 1914, p. 241; Standley, 1917, p. 111).

About half of the specimens here included had been labelled *A. hybridus;* the rest had been given a wide variety of names, among which *A. chlorostachys* Willd. was prominent. This is one of the many names which Thellung reduced to synonymy with *A. hybridus*.

Northern Race of A. hybridus.—This race is common as a weed in the eastern United States and has been found at scattered places in the Old World. Specimens have been examined from Massachusetts, Connecticut, New York, New Jersey, Pennsylvania, the District of Columbia, Virginia, West Virginia, South Carolina, Florida, Mississippi, Ohio, Indiana, Kentucky, Illinois, Missouri, Arkansas, Kansas, Oklahoma, and Texas; also from Bermuda, the Bahamas, Japan, China, Algeria, Morocco, and Australia.

The inflorescences ordinarily have a great many short, crowded, lateral spikes, as in *A. retroflexus*, but the spikes are much less stiff and much less thick. The bracts are quite long, and the rather slender midribs extend far beyond the laminas. The tepals are about as long as the fruit, slightly recurved and often lightly indurated at the bases. The outer tepals are oblong and acute-tipped, the inner slightly obovate and acutish-tipped. The utricle cap narrows to a tower below the style-branches; the style-branches are erect and their bases are slender, meeting in a shallow cleft.

Individual specimens often show definite divergence from the norm of the race, both in superficial appearance and in flower characters. I believe that much of this variation is produced by introgression from *A. retroflexus*. Mass collections from weed amaranth populations around St. Louis (*J. D. Sauer 1473*, 50 plants; *1483*, 30 plants; etc.) include a continuous series of intermediates between the two

species. In some of these Missouri weed populations hybridization between *A. hybridus* and the genus *Acnida* is also indicated (*J. D. Sauer 1482*, 25 plants; etc.). Hybrids between *Amaranthus* and *Acnida* have been produced artificially by Murray (1940a).

Tropical Race of A. hybridus.—This race is a common weed from Mexico through Central America into northern South America and is scattered widely elsewhere. Specimens have been examined from the states of Nuevo León, San Luis Potosí, Nayarit, Jalisco, Colima, Michoacán, México, Puebla, Vera Cruz, Tabasco and Oaxaca in Mexico; from Guatemala; El Salvador; Costa Rica; the departments of Tachira, Mérida, and the Distrito Federal in Venezuela; La Paz and Cochabamba in Bolivia; the states of São Paulo and Minas Geraes in Brazil; the Dominican Republic; and Algeria.

In its inflorescence and flower characters, this race is much like the northern race of the species. The most tangible difference is in the utricle cap and style-branches. In the tropical race, the utricle cap tapers more gradually and is not constricted into a definite tower; the bases of the style-branches are farther apart and form more of a saddle than a cleft.

There is more variation between individual specimens included in this race than in any other of the entities examined. Even within what may be regarded as the core of the group, there are many subtle variants. Ranged around this indistinct core is a bewildering variety of divergent individuals, scarcely any two of which are exactly alike, even within a single collection. These specimens, not clearly assignable to any species, are not cited in the Specimens Examined on pages 620–623.

A few of these divergent individuals appear to be intermediate between *A. hybridus* and the grain species: *A. leucocarpus* is approached by some Mexican specimens (e.g. *J. D. Sauer 1313*), *A. cruentus* by some Central American specimens (e.g. *Standley 59046*). Other individuals approach some of the non-cultivated species of the section: *A. retroflexus* in northeastern Mexico (e.g. *Gregg 283*), *A. scariosus* in southern Mexico and Guatemala (e.g. *Pringle 6735*), *A. dubius* in Central America (e.g. *Pittier & Durand 3534*), and *A. quitensis* in Bolivia (e.g. *Bro. Julio 136*). Moreover, there is a bewildering series of forms, often labelled *A. hybridus* in herbaria, which appear to be intermediate between *A. hybridus* and species in other sections of the genus. This heterogeneous group includes specimens from wide areas of North, Central, and South America. Some of them diverge from typical *A. hybridus* in habit and inflorescence aspect, some have indehiscent fruits, almost all have reduced tepal or stamen number or both.

This complex of divergent forms related to *A. hybridus* cannot be satisfactorily analyzed here. Description and illustration of the collected variants, which probably represent only a small sample of the actual diversity, would require more space than all the preceding entities. Moreover, a much greater density of collections, together with mass samples of critical populations, are needed for an

understanding of this group. With the available material, I could do no more than speculate as to which variants are of hybrid origin and which are stable entities deserving taxonomic recognition.

Amaranthus Powellii S. Wats.—

This species characteristically has fewer than 5 stamens and therefore would be excluded from the section AMARANTHOTYPUS as usually defined. However, in other characters it is too close to some of the species of the section to be ignored here.

Like *A. leucocarpus*, *A. Powellii* was described by Watson (1875, p. 347) from plants grown at Harvard from Powell's wonderful packet of Arizona seeds. Unlike *A. leucocarpus*, this species has since been collected in abundance. It has been generally recognized by American workers (Uline and Bray, 1894, p. 313; Standley, 1917, p. 112; and others). A minor species from New Mexico, *A. bracteosus*, has been described as distinct from *A. Powellii* (Uline and Bray, 1894, p. 314), but examination of the type collections of both species reveals no impressive differences. I believe *A. bracteosus* should be reduced to a synonym of *A. Powellii*.

The specimens included here had mostly been labelled as either *A. Powellii*, *A. hybridus*, or *A. retroflexus* in about equal proportions.

Great Basin Race of A. Powellii.—This race, which includes the type of the species, is common as a weed and is occasionally reported in natural habitats over much of the western United States and northern Mexico. It has been found mostly at high elevations, often between 2,000 and 3,000 meters, in dry regions. Specimens are available from Wisconsin, Texas, Wyoming, Colorado, New Mexico, Arizona, Idaho, Utah, Washington, Oregon, California, and from the Mexican states of Coahuila, Chihuahua, and Baja California.

The inflorescences characteristically have a quite long, erect, terminal spike and a few erect lateral spikes; the spikes are thick and stiff and have a very prickly appearance from the exceptionally long bracts. The bracts are similar to those of *A. retroflexus*, with a very heavy midrib and a large lamina extending well toward the tip.

In other characters, this group is quite distinct from *A. retroflexus*. There are usually three or four stamens, although some flowers with five stamens can be found on a good many individuals. Tepal number in both staminate and pistillate flowers usually varies from four to five. The tepals are usually a little longer than the utricle, straight or slightly recurved, and somewhat indurated at their bases. The outer tepals are oblong or ovate, and acute-tipped; the inner are oblong or slightly obovate, and acutish or somewhat obtuse at the tips. The utricle cap tapers to the style-branches. The style-branches are of medium length and slightly recurved; their thick bases form a shallow cleft.

Variation in flower characters within this race is not great.

Cordilleran Race of A. Powellii.—This race is common as a weed in California and has been collected infrequently but very widely in Latin America, particularly at high elevations. Specimens are available from the states of Sonora, Chihuahua, San Luis Potosí, Tamaulipas, Michoacán, and Puebla in Mexico; Ecuador; Peru; Chile; La Paz in Bolivia; and Tucumán in Argentina.

This race is very similar to the preceding race in most characters, and probably cannot be clearly separated from it. It differs in having somewhat longer and more acute tepals, which are seldom recurved, and longer style-branches with thicker bases.

Other Closely Related Species.—

The existence of reduced stamen and tepal numbers in *A. Powellii*, as well as in some aberrant forms of *A. hybridus*, raises a question about the definition of the section AMARANTHOTYPUS.

The section was originally defined to include only a few adventive American species present in Europe; these were all sharply distinct from the native species. The section retains clear definition, as in Thellung's treatment (1914), only so long as consideration is limited to species present in the Old World. I know of no generally recognized or recognizable species peculiar to the Old World which is not distinguishable from all the species of AMARANTHOTYPUS by several qualitative characters. However, sharp definition of the section disappears when all the American species are considered. Among the New World endemics, there are a great many generally recognized species which are transitional; they are obviously closely related to AMARANTHOTYPUS, but lack one of the characters of the section. For example, *A. Palmeri* S. Wats., a common weed amaranth of the drier parts of the United States and Mexico, differs from species of AMARANTHOTYPUS chiefly by being dioecious; *A. Wrightii* S. Wats., a minor endemic of the southwestern states, differs only by its reduced stamen and tepal number; *A. chihuahuensis* S. Wats., a north Mexican endemic, only by its lack of a terminal spike; *A. ataco* Thellung, of Chile and Argentina, only by its indehiscent fruit. There are various similar examples of North and South American species which would be excluded from the section by a single character.

A considerable amount of material of these border-line species has been examined. None of it appears to be particularly close to any of the grain amaranths and it will not be discussed here. Once the rather arbitrary limits of the section AMARANTHOTYPUS are passed, there seems to be no natural stopping place short of a complete study of all the American species of *Amaranthus*.

III. CONCLUSIONS

The grain amaranths belong to several distinct but closely-related species, cultivated by a curiously diverse and scattered group of peoples since immemorially ancient times. Only a rough outline of the complex history of these ancient plants can be given in this preliminary survey.

In the Americas there are four major grain amaranth regions, each with its own peculiar cultivated species. *Amaranthus leucocarpus* dominates the great Mexican center and its tenuous extension into the southwestern United States. *Amaranthus cruentus* is cultivated in Guatemala, *A. caudatus* in the Andes, and *A. edulis* in Argentina. There seems to have been some diffusion of species between the Mexican and Guatemalan centers and between the Andean and Argentine centers, but on the whole the ranges of the species in the New World are distinct.

In Asia there is a great, vaguely delimited grain amaranth region stretching all the way from Manchuria through interior China and the Himalaya to Afghanistan and Persia. *Amaranthus leucocarpus* and *A. caudatus* are both grown throughout this area. The poorly known grain crop of Africa is probably also *A. caudatus*.

In mode of cultivation and use, the Old and New World crops are strikingly similar. In both areas the crop shows a special affinity for the highlands; so far as I know, its concentration at high elevations is not explainable by any natural barriers. Many wild amaranth species are common in the lowlands, and the grain species themselves are widely grown down to sea level as ornamentals. In both the Old and New World, the plants are usually grown on a small scale, mixed in the plantings of maize and other crops. The grain is ordinarily consumed by the growers and is prepared in similar ways almost everywhere. The seeds are first parched or popped; then they are either made into balls like popcorn, with a syrup binder, or they are ground to meal, which is stirred into a drink or baked into little cakes.

Taxonomically, all of the grain amaranths cultivated in the Old World are indistinguishable from certain of those cultivated in the New World. Not only in terms of species, but also in terms of sub-specific entities, the available Old World specimens represent nothing but a small sample of the diversity present in the American grain amaranths. There is an important group of cultivated amaranths which are obviously natives of Asia, including *A. tricolor*, *A. melancholicus*, *A. mangostanus*, *A. gangeticus*, etc. However, these are grown exclusively as pot-herbs or ornamentals, apparently never for the seeds. This entire Asiatic pot-herb group is easily distinguishable from the grain group by important technical characters, such as number of stamens, number of tepals, and shape of the tepals. Few of these Asiatic species are even superficially similar to the grain amaranths; for one thing, none of them has a branched terminal inflorescence.

The non-cultivated amaranths closely related to the grain species also show a striking concentration in the New World. There are many entities in this section of the genus which are endemic to the Americas; some are weeds, some appear to be truly wild. No evidence was found, either in the literature or in the herbarium, of any non-cultivated entity closely related to the grain amaranths which is peculiar to the Old World. Except in the Americas, members of this section of the genus are ordinarily found outside of cultivation only as sporadic adventive weeds.

The conclusion appears inescapable that the grain amaranths are all of New World origin. From which wild species they were derived is less clear. The grain species are all cultigens, unknown in the wild except as infrequent escapes. *Amaranthus leucocarpus* is morphologically fairly close to two non-cultivated species, *A. hybridus* and *A. Powellii*, both widespread in North and Central America. *Amaranthus cruentus* is more like *A. dubius* of Central America and the West Indies, while *A. caudatus* and *A. edulis* are closer to a South American wild species, *A. quitensis*. I am unable even to guess as to whether the cultigens were derived from these or similar wild species by simple selection or whether they are of complex hybrid origin.

The sharp taxonomic separation found between the cultivated species and their closest wild relatives was completely unexpected, since the frequency of hybridization in this genus is well known. The discontinuity may be explainable by the almost universal practice of selecting pale seeds for planting. No analysis of the genetics of the seed color is available, but it seems likely that the pale-seeded cultivated forms are simple recessives. If so, elimination of dark seeds in planting should be an effective barrier against introgression from wild species, which are without exception dark-seeded.

The cultigens differ from the wild species, not only in characters which are probably simple genetically, such as seed color, but also in quantitative characters, particularly those affecting grain yield. The higher yield of the cultivated species results mostly from the greater number of flowers and seeds produced, rather than from larger seed size. The cultigens are strikingly bigger in plant size than the wild species; they have more inflorescences per plant and the inflorescences are enormously larger and more compound. A well-developed grain amaranth produces such an enormous quantity of seed, though the seeds are individually minute, that the yield of the crop per unit area often exceeds that of maize, according to the few published statistics on yield and the opinions of Latin American farmers with whom I have talked.

Development of these stable entities so distinct from their wild relatives would be expected to require long selection. The antiquity of the crop is also indicated by other evidence. In both Asia and the Americas the crop has almost invariably been reported as a declining and disappearing relic, conserved mostly in remote primitive communities. Abundant direct evidence of the antiquity of the crop is available for the New World. In addition to the archaeologic cache of *A. caudatus* fruits found in South America, there are the magnificent early documentary records from Mexico. These indicate that grain amaranths were one of the great food staples of Mexico at the time of the Conquest, regarded by the people as among their most ancient crops, and fantastically important in legend and ritual.

The question as to whether the crop reached Asia before the European expansion cannot be answered with certainty. There is the 10th-century Chinese document which seems to refer to grain amaranths, but this is hardly absolute proof. If the crop was introduced into Asia after Columbus, it must be credited with a

remarkable achievement in making itself very much at home among strangers within a few generations. Of course, if these people were accustomed to cultivate one species of grain amaranth, rapid adoption of a second species would not be so remarkable. Of the two species grown for grain in Asia, *A. leucocarpus* is the more common and widespread and might be supposed to be more ancient in the area. Strangely enough, plants resembling *A. leucocarpus* do not appear in the European herbals until about 1700, more than a century after *A. caudatus* had been brought to Europe as an ornamental.

We have seen that the practice of cultivating grain amaranths is old and deep in various cultures. I believe these plants deserve special consideration by those willing to speculate about the very beginnings of agriculture. Various workers have inclined to the idea that the transition of plants from wild to domesticated was not always accomplished in a single step by deliberate domestication. In many cases wild plants may have become weedy camp-followers and entered cultivation gradually through a long process of modification by largely unconscious human selection. One version of this concept has been well expressed by Frazer (1912, 1:128). He postulated that by digging up the soil in a search for roots, ancient man produced favorable growing plots for his wild food seeds, dropped accidentally during winnowing or other operations. A slightly different version than Frazer's would involve the accidental establishment of useful plants on village refuse heaps. In either case, by continued harvesting and accidental sowing, plants able to persist in such disturbed habitats might become domesticated by imperceptible degrees. The amaranths are attractive candidates for such accidental domestication; the seeds of the wild species are often gathered and eaten by primitive peoples and the plants are notoriously successful weeds of disturbed habitats.

Following another line of reasoning, Carl Sauer (1936, p. 292) pointed out that the presence side by side in an area of two starch crops, one localized and the other of wide range, suggests that the local crop is older in the area; it can survive as a relic because of tradition and the inertia of habit. "Qualities that are insufficient to cause the development side by side of two similar foodstuffs from different wild ancestors may be sufficient to keep one in use if a more valuable crop is brought in from another area." This line of reasoning suggests that grain amaranths, at least in some areas, are relics of an ancient staple starch crop, largely supplanted by a later arrival, maize.

Such speculations will obviously need additional support from factual evidence if they are to become more than hypotheses. Such evidence may eventually come from analysis of pollen deposits. Deevey (1944, p. 149) made a suggestive preliminary pollen analysis of sediments in Lake Pátzcuaro in Michoacán, Mexico. He estimated that the sediments are now accumulating at the rate of about one meter in 400 years, but that deposition was probably slower in the past. Maize and agave pollen were found down to depths of between four and five meters. About a meter lower, he found that there had been a sudden increase in deposition of a type of pollen identified only as coming from either chenopods or amaranths. More

precise identification of this pollen would be extremely interesting. It may be derived from wild amaranths or chenopods, as Deevey assumes. On the other hand, it may mark the coming of an agriculture based on grain amaranth cultivation. When the first Spanish conquerors arrived on the shores of this same lake, some thousands of years after this pollen was deposited, they found that the Indians had the custom of making little figures of amaranth meal for the festival of their earth goddess, giver of all crops.

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List of Specimens Examined

Supposed hybrids and specimens of *Amaranthus* without collector's numbers are not cited. Letters in parentheses refer to herbaria from which the specimens were obtained: GH—Gray; MO—Missouri Botanical Garden; UC—University of California; US—U. S. National; X—undistributed specimens. Italicized letters refer to species determinations: *Bi—A. Bigelovii; Br—A. Brandegei; Ca—A. caudatus; Ce—A. celosioides; Cr—A. cruentus; D—A. dubius; E—A. edulis; H—A. hybridus; L—A. leucocarpus; P—A. Powellii; Q—A. quitensis; R—A. retroflexus; S—A. scariosus; V—A. viscidulus.*

United States and Canada.—

Abrams, L. R. *2963* (MO) *P.*
Allard, H. A. *9606* (MO) *H.*
Allen, Paul. *142* (MO) *P.*
Anect, Bro. *138* (MO) *P.*
Arthur, J. C. *8* (MO) *R.*
Austin, S. W. *372* (UC) *R.*
Baker, C. F. *303* (MO) *P.*
Baker, Earle & Tracy. *486* (MO) *P.*
Ball, C. R. *531* (MO) *R*; *588* (MO) *R.*
Bechtel, A. R. *8057* (MO) *R.*
Bell, W. B. *280* (MO) *R.*
Benke, H. C. *5798* (MO) *H*; *5799* (MO) *R.*
Berkley, E. E. *1283* (MO) *R*; *1482* (MO) *H.*
Blumer, J. C. *1404* (MO) *P.*
Boettcher, F. L. J. *209* (MO, UC) *R.*
Booth, L. M. *1295* (UC) *P.*
Bowerman, M. L. *3539* (UC) *R*; *3727* (UC) *R.*
Braunton, E. *705* (UC) *P*; *720* (UC) *P*; *1105* (MO) *R.*
Brooks, S. C. *1065* (UC) *H.*
Burk, M. *670* (MO) *R.*
Bush, B. F. *316* (UC) *H*; *317* (UC) *R*; *428* (MO) *H*; *447* (MO) *H*; *476* (MO) *H*; *485* (MO) *R*; *789* (MO) *H*; *8104* (MO) *R*; *8198* (UC) *R*; *9050C* (UC) *R*; *13118* (MO) *H*; *13119* (MO) *H*; *13173* (MO) *H*; *13174* (MO) *H*; *13208* (MO) *H*; *13209* (MO) *H*; *15772* (MO) *H*; *15782* (MO) *H.*
Carr, W. P. *142* (MO) *R.*
Clark, J. A. *141* (MO, UC) *R, P.*
Clarke, D. G. *58* (MO) *R.*
Clemens, J. *11561* (MO) *R.*
Coghill, G. E. *161* (MO) *P.*
Cooke, W. B., II. *553* (UC) *P.*
Coues & Palmer. *41* (MO) *P.*
Cowen, J. H. *2153* (UC) *R.*
Craig, M. *4411* (UC) *R.*
Cronquist, A. *3429* (MO) *P*; *3831* (MO) *P.*
Curtiss, A. H. *4982* (MO) *H.*
Cutak, L. & Christ, A. *100* (MO) *R.*
Darrow, Phillips & Pultz. *1179* (UC) *P.*
Davis, J. *591* (MO) *H*; *2025* (MO) *H*; *2078* (MO) *R*; *3031* (MO) *H*; *3473* (MO) *H*; *4028* (MO) *H.*
Davy, J. B. *4044* (UC) *P*; *7050* (UC) *P.*
Demaree, D. *7563* (MO) *R*; *8427* (MO) *H*; *8801* (MO) *H*; *13261* (MO) *R*; *13405* (MO) *R*; *18459* (MO) *H*; *20398* (MO) *H*; *21675* (MO) *H.*
Dudgeon, W. S. *17* (MO) *R.*
Ellis, C. C. *146* (MO) *P.*
Fendler, A. *735* (MO, US) *P*; *736* (MO) *R.*
Fogg, J. M., Jr. *1402* (MO) *R.*
Gates, F. C. *18859* (MO) *R.*
Goehring, G. H. M. *67* (MO) *H.*
Goodner & Henning. *1157* (MO) *P.*
Gould & Hudson. *3788* (UC) *P.*
Gould & Robinson. *4998* (UC) *P.*
Grant, G. B. *1718* (MO) *P*; *6577* (MO) *P.*
Greenman, J. M. *1599* (MO) *H.*
Greenman & Greenman. *3733* (MO) *H.*
Hansen, G. *1260* (MO) *P*; *1411* (UC) *P.*
Hanson, H. C. *A157* (MO) *P.*
Harrison & Harrison. *8573* (MO) *P.*
Heiser, C. B., Jr. *1919* (UC) *R.*
Heller, A. A. *1765* (MO, UC) *R*; *12199* (MO) *R.*
Heller & Heller. *3428* (MO, UC) *P.*
Hoover, R. F. *99* (UC) *R.*
House, H. D. *29425* (MO) *H*; *30165* (MO) *R.*
Johnston, E. L. *287* (MO) *R.*
Jones, M. E. *3977* (MO, UC, US) *P*; *6050g* (MO, UC) *P.*
Kellogg, J. H. *511* (MO) *H*; *888* (MO) *H.*
Kerr, M. *46* (UC) *P.*
Killip, E. P. *40186* (MO) *H.*
Leiberg, J. B. *1550* (MO, UC) *P.*
Mackensen, B. *10* (MO) *R.*
Mackenzie, K. K. *4775* (MO) *H.*
McKnight, K. *10704* (UC) *P.*
Mead, S. B. *14* (MO) *H.*
Metcalf, F. P. *1342* (MO) *R*; *6395* (MO) *H.*
Meyer, F. G. *786* (MO) *P.*

Moldenke, H. N. *499* (MO) *H.*
Moore, A. H. *355* (UC) *R*; *4351* (GH) *L.*
Mueller, C. H. *7986* (MO) *P.*
Muenscher, W. C. *16104* (UC) *P.*
Mulford, A. I. *381* (MO) *P*; *747* (MO) *R.*
Nelson, A. *8079* (MO) *P.*
Norton, J. B. *424* (MO) *R*; *425* (MO) *H.*
Orcutt, C. R. *5868* (MO) *R.*
Palmer, E. 1875:319 (UC) *P*; *1892:2716* (UC) *R.*
Palmer, E. J. *427* (MO) *H*; *2624* (MO) *H*; *3114* (MO) *R*; *12292* (MO) *R*; *30741* (MO) *P*; *46377* (MO) *R.*
Pammel, L. H. *48* (MO) *R*; *3863* (MO) *R.*
Parish, S. B. *11657* (UC) *P.*
Parry, Bigelow, Wright & Schott. *1190* (US) *Bi.*
Pendleton, R. L. *191* (UC) *P.*
Redfield, J. H. *7020* (MO) *H.*
Reverchon, J. *1756* (MO) *R*; *2939* (MO) *R.*
Ricksecker, A. E. *60* (UC) *R.*
Rydberg & Imler. *647* (MO) *R.*
Sauer, J. D. *1189* (X) *H*; *1237* (MO) *P*; *1238* (MO) *R*; *1459* (X) *H*; *1469* (MO, UC) *R*; *1470* (MO, UC) *P*; *1471* (UC) *R*; *1472* (MO, UC) *P.*
Schreiber, B. O. *741* (UC) *P.*
Sherff, E. E. *1845* (MO) *R.*
Standley, J. P. *232* (MO) *R.*
Standley, P. C. *4535* (MO) *P*; *4891* (MO) *P*; *4918* (MO) *P*; *5149* (MO, US) *V.*
Stanford, E. E. *703* (GH) *Cr.*
Stevens, G. W. *859* (MO) *R*; *1841.2* (MO) *H.*
Steyermark, J. A. *8875* (MO) *H*; *8972* (MO) *R.*
Thompson, C. H. *137* (MO) *R.*
Thompson, J. W. *3664A* (MO) *P.*
Tracy, S. M. *2170* (MO) *H*; *2173* (MO) *H.*
Wahl, H. A. *4763* (UC) *P*; *6257* (UC) *P.*
Walker, H. A. *772* (UC) *P.*
Waugh, —. *164* (MO) *R.*
Wiegand, K. M. *6396* (GH, MO) *L.*
Wislizenus, F. *357* (MO) *H.*
Wooton, E. O. *73* (MO, UC) *R*; *300* (US) *V*; *3950* (US) *V.*
Wright, C. *1748* (MO) *P*, in part.

Mexico and Central America.—

Allen, P. H. *874* (US) *D.*
Alvarez, C. *749* (GH) *H.*
Arsène, Bro. G. *374* (US) *Cr*; *397* (US) *P*; *1052* (US) *P*; *2300* (MO, US) *P.*
Baker, —. *2873* (UC, US) *Cr.*
Botteri, M. *261* (US) *H*; *332* (GH) *H*; *401* (GH) *H*; *553* (GH, US) *H*; *555* (GH) *H.*
Calderón, S. *739* (US) *Cr*; *2090* (US) *S.*
Cooper, J. J. *68* (US) *H.*
Deam, C. C. *210* (GH) *S.*
Erlanson, C. O. *350* (US) *D.*
Ervdenberg, L. C. *283* (GH) *H.*
Fisher, G. L. *45129* (US) *P.*
Garnier, A. *369* (US) *S*; *371* (US) *Cr*; *525* (US) *S*; *1765* (GH) *S.*
Gaumer, G. F. *1788* (MO) *D*; *1789* (MO) *D*; *23548* (MO) *S*; *23550* (MO, UC, US) *D*; *23735* (UC) *S*; *23789* (US) *D*; *24065* (MO) *D.*
Gentry, H. S. *1843* (MO, UC) *L*; *1844* (US) *L*; *6547* (MO) *L.*
Gonzalez & Conzatti. *909* (GH) *Cr.*
Grant, V. *934* (GH) *S.*
Hernandez X., E. *3715* (X) *L.*
Heyde, E. T. *720* (US) *H.*
Hinton, G. B. *2137* (MO, US) *L*; *3015* (GH, US) *H*; *13584* (GH) *H.*
Hunter & Allen. *712* (MO) *D.*
Hunziker, A. T. *2948* (GH) *L.*
Johnson, H. *839* (US) *Cr.*
Johnston, I. M. *8342a* (GH) *R.*
Killip, E. P. *3209* (US) *D*; *3432* (US) *D.*
Le Sueur, H. *611* (GH, MO) *P*; *612* (GH) *P.*
Lumholtz, C. *1041* (GH, US) *P.*
Lundell, C. L. *5200* (US) *P.*
Martinez-Calderón, G. *96* (US) *H.*
Mell, C. D. *2070* (US) *D.*
Mexia, Y. *41* (MO) *D.*
Meyer & Rogers. *2814* (X) *P.*
Padilla, S. A. *148* (MO, US) *S*; *421* (US) *S.*
Palmer, E. *1880:1128* (US) *R*; *1880:-2043* (GH) *R*; *1886:626* (MO) *H*; *1886:629* (US) *H*; *1886:630* (MO) *H*; *1886:694* (US) *L*; *1886:695* (US) *L*; *1891:1000* (GH) *Br*; *1891:1718* (US) *Cr*; *1892:1883* (US) *H*; *1892:1884* (GH) *H*; *1894:142* (US) *S*; *1897:126* (US) *H.*
Parry & Palmer. *785½* (GH, MO) *H.*
Paul, Bro. *76* (US) *D.*

Piper, C. V. *5782* (US) *D.*
Pittier, H. *197* (US) *L*; *3610* (US) *D*; *6859* (US) *D.*
Pringle, C. G. *2179* (GH) *P.*
Purpus, C. A. *7787* (UC) *H*; *8665* (MO, UC, US) *S*; *8871* (MO, UC) *H*; *10831* (US) *H.*
Renson, C. *288* (US) *H.*
Rovirosa, J. N. *744* (US) *H.*
Sauer, C. O. *28* (MO, UC) *H.*
Sauer, J. D. *1010* (MO) *Ca*; *1112* (MO, UC) *P*; *1133* (X) *H*; *1141* (X) *H*; *1150* (MO) *H*; *1153* (MO) *H*; *1155* (X) *H*; *1161* (MO) *L*; *1162* (MO) *L*; *1168* (X) *Cr*; *1170* (MO) *L*; *1171* (MO) *L*; *1172* (MO) *Cr*; *1173* (MO) *L*; *1174* (MO) *L*; *1175* (MO) *Cr*; *1176* (MO) *Cr*; *1177* (X) *Cr*; *1193* (MO) *L*; *1239* (X) *L*; *1240* (MO) *Cr*; *1265* (MO) *Cr*; *1266* (MO) *Cr*; *1267* (X) *Cr*; *1274* (X) *L*; *1277* (X) *L*; *1285* (MO) *Cr*; *1311* (X) *Cr*; *1355* (MO) *L.*
Schery, R. W. *131* (MO) *P.*
Seaton, H. E. *19* (GH) *H.*
Smith, C. L. *1768* (GH) *H.*
Solis Rojas, F. *250* (MO) *H.*
Standley, P. C. *19238* (US) *Cr*; *20712* (MO, US) *S*; *20833* (MO, US) *S*; *21111* (US) *S*; *24286* (US) *D*; *25670* (US) *D*; *26107* (US) *D*; *26891* (US) *D*; *27101* (US) *D*; *28192* (US) *D*; *28517* (US) *D*; *29840* (US) *Cr*; *30135* (US) *D*; *30254* (US) *D*; *30596* (US) *Cr*; *31485* (US) *D*; *37004* (US) *D*; *39028* (US) *D.*
Standley & Valerio. *44258* (US) *S.*
Stanford, Retherford & Northcraft. *173* (MO) *P*; *505* (UC) *P.*
Stork, H. E. *89* (US) *D.*
Tonduz, A. *7118* (US) *H*; *13704* (US) *S.*
Townsend & Barber. *238* (MO, US) *P.*
Tuerckheim, H. von. *11774* (US) *Cr.*
Wedel, H. von. *2854* (MO, US) *D.*
White, G. *119* (MO) *D.*
White, S. S. *1592* (GH) *H*; *3393* (GH) *P.*
Wiggins & Demaree. *4789* (UC, US) *P.*
Wiggins & Gillespie. *4114* (MO, US) *P.*
Wislizenus, F. *215* (MO) *Cr.*

West Indies.—

Barreto, M. *4* (US) *Cr.*
Broadway, W. E. *5553* (GH, MO, UC) *D*; *6802* (GH, MO, US) *D*; *7967* (MO) *D.*
Brown, S. *538* (US) *H.*
Brown & Britton. *370* (US) *H.*
Brown, Britton & Bisset. *1989* (US) *H*; *2231* (US) *H.*
Collins, F. S. *111* (GH) *H*; *188* (GH) *H*; *189* (US) *H.*
Curran & Haman. *66* (UC) *D.*
Ekman, E. L. *H9828* (US) *Cr*; *H12616* (US) *Cr*; *H13914* (US) *H.*
Hermann, —. van. *5102* (US) *D.*
Holdridge, L. R. *1025* (US) *Cr.*
Jack, J. G. *6119* (US) *D.*
Leonard, E. C. *7619* (US) *Cr*; *8359a* (UC, US) *D*; *9410* (MO) *D.*
Leonard & Leonard. *15302* (US) *Cr.*
Moore, A. H. *2948* (GH) *H.*
Orcutt, C. R. *323* (UC) *D*; *1869* (UC) *D*; *2722* (UC) *D.*
Otero, J. I. *48* (MO) *D.*
Ricksecker, A. E. *109* (MO, UC, US) *D*; *332* (MO) *D.*
Robinson, B. L. *37* (GH) *H.*
Shafer, J. A. *12045* (MO) *D.*
Sieber, F. W. *159* (MO) *D.*
Sintenis, Bro. *3553* (GH) *D.*
Stevenson, J. A. *5298* (US) *Cr.*
Valeur, E. J. *231* (MO) *D.*
Wilson, P. *392* (US) *D.*

South America.—

Archer, W. A. *2677a* (US) *D.*
Ariste-Joseph, Bro. *A359* (US) *Cr.*
Bang, A. M. *97* (GH, MO, US) *P*; *231* (US) *H*; *732* (US) *H*, in part.
Barkley, Barros & Alvarez. *395* (X) *D.*
Bartlett, H. H. *20319* (US) *Q.*
Buchtien, O. *3166* (US) *Q*; *3168* (GH, US) *Q*; *4198* (GH) *H*; *5402* (US) *Ca*; *8785* (US) *P.*
Campos Novaes, J. de. *430* (US) *Cr.*
Cardenas, M. *3512* (GH, US) *Ca*; *3513* (GH) *Ca*; *3514* (GH) *Ca*; *3515* (GH) *Ca*; *3516* (GH) *H.*
Cook & Gilbert. *256* (US) *Ca.*
Cuatrecasas, J. *14471* (MO) *D.*
Daniel, Bro. *447* (US) *D.*
Ekman, E. L. *117* (US) *Q*; *118* (GH) *Q.*
Elias, Bro. *1483* (US) *Cr.*
Fendler, A. *1760* (GH) *H*; *2386* (GH) *Cr, D.*
Firmin, Bro. G. *214* (US) *P.*
Grisales, A. *11* (X) *Cr.*
Hassler, E. *12506* (MO, US) *Q.*
Heriberto, Bro. *56* (US) *D.*
Herrera, F. L. *1053* (GH, US) *P*; *1073* (US) *P.*
Herter, G. *54* (UC) *Q*; *54a* (MO) *Q*; *54b* (US) *Q*; *805* (GH) *Q.*

Houk, W. G. *61* (US) *H.*
Huidoho, K. de. *439* (US) *Q.*
Hunziker, A. T. *810* (US) *Ca; 1085* (GH) *Ca; 2127* (GH) *E; 2128* (GH) *Ca; 3003* (MO) *E.*
Jörgensen, P. *2563* (US) *Q; 2574* (MO, US) *Q; 3441* (MO, US) *Q.*
Killip & Smith. *21926* (US) *Ce.*
Krapovickas, A. *2260* (GH) *Q.*
Lehmann, F. C. *7702* (GH, US) *Cr.*
Mandon, G. *1018* (GH) *Q,* in part.
Mille, A. *46* (GH) *Ce.*
Miller & Johnston. *30* (MO) *D.*
Monetti, —. *1311* (GH) *Q; 1653* (GH) *Q; 1718* (GH) *Q; 2271* (GH) *Q.*
Montero, G. *2303* (GH) *P.*
Morong, T. *980* (UC, US) *Q.*
Noguera, J. M. *49* (GH) *D.*
Pachano, A. *171* (GH, US) *Cr.*
Parodi, L. R. *8910* (GH) *Q.*
Peirano, —. *9666* (GH) *Q.*
Pennell, F. W. *4668* (GH) *D.*
Pickel, B. *3268* (US) *Cr.*
Potter, D. *5334* (GH) *D.*
Rodriguez, —. *185* (GH) *Q.*
Santoro, J. *408* (US) *H; 485* (US) *H.*
Sauer, J. D. *1179* (X) *Ca; 1241* (MO) *Ca; 1283* (MO) *Ca; 1298* (X) *Ca; 1314* (X) *Ca; 1315* (X) *Ca.*
Smith, H. H. *1194* (UC) *D; 1195* (MO) *D.*
Snodgrass & Heller. *219* (GH) *Q.*
Soukup, J. *1999* (US) *P.*
Steinbach, —. *2793* (GH) *H.*
Tamayo, F. T. *513* (US) *H; 2472* (US) *H.*
Tomas, Bro. *906* (US) *D.*
Venturi, S. *1954* (US) *Q,* in part; *1955* (US) *Q; 2044* (US) *Q; 4234* (GH) *Q; 6038* (MO, US) *Q; 10316* (GH) *Q.*
Weberbauer, A. *5332* (GH) *Ce.*
Williams, L. O. *5653* (GH) *Cr.*
Williams & Assis. *6461* (GH) *H.*

Asia.—

Amdursky, J. *231* (US) *R.*
Beach, K. H. *47* (UC) *R; 125* (UC) *R.*
Boeea, R. S. *6491* (GH) *Cr; 8022* (GH, US) *Cr; 8710* (GH) *Cr.*
Castro & Melegrito. *144* (UC) *Cr.*
Chen, F. H. *369* (GH) *Ca.*
Chen, Y. *803* (UC) *L; 898* (UC) *L; 928* (UC) *L.*
Chiao, C. Y. *333* (UC) *L; 1183* (UC, US) *Cr; 3143* (UC) *L.*
Ching, R. C. *4668* (UC, US) *Cr.*
Clemens & Clemens. *3309* (UC, US) *Cr.*
Cowgill, W. H. *2087* (GH) *Ca; 2354* (GH) *L; 2355* (GH) *L.*
Devore & Hoover. *112* (US) *Cr.*
Dorsett & Dorsett. *4089* (UC, US) *L.*
Elliott, E. *14* (GH, US) *H.*
Fang, W. P. *3242* (GH, US) *L.*
Feng, H. T. *16* (UC) *Cr.*
Field & Lazar. *807* (GH, US) *R; 997* (GH, US) *R.*
Groff, G. W. *711* (UC) *Ca.*
Henry, A. *2732* (US) *L; 4808* (GH) *L.*
Hooker, J. D. *2435* (GH) *L.*
Koelz, W. *7279* (US) *L.*
Liu, J. C. *823* (UC) *R; 1716* (UC) *R.*
Maire, E. E. *503* (UC) *L; 504* (UC) *L; 509* (UC) *H; 712* (UC) *L.*
McClure, —. *3345* (UC) *Cr.*
Merrill, E. D. *8501* (US) *Cr.*
Ritchie, —. *631* (GH) *L.*
Rock, J. F. *6283* (UC, US) *L.*
Sauer, J. D. *1310* (X) *Ca; 1484* (MO) *L; 1489* (MO) *L; 1492* (X) *L; 1495* (MO) *L; 1499* (X) *L; 1503* (MO) *Ca; 1505* (MO) *Ca.*
Schlagintweit, —. *1486* (GH) *Ca; 1958* (GH) *L; 3293* (GH) *L; 9364* (GH) *L; 12075* (GH) *L; 2:1353* (UC) *L; 2:4365* (UC) *L; 4:871* (UC) *L; 4:872* (US) *Ca; 4:5787* (US) *Ca; 4:5789* (US) *L; 4:6407* (US) *L; 4:13177* (US) *L.*
Shiota, K. *2667* (GH) *Ca; 2670* (GH) *Cr; 2672* (GH) *R.*
Steward, Chiao & Cheo. *784* (GH, US) *L.*
Stewart, R. R. *19656* (GH) *L; 21360* (GH) *R.*
Strachey & Winterbottom. *2* (GH) *Ca,L.*
Vvedensky, —. *425* (MO) *R.*
Zimmerman, —. *254* (US) *L.*

Africa.—

Craine, —. de. *736* (GH) *Ca.*
Dümmer, R. *532* (US) *Cr; 590* (US) *Cr.*
Jamin, P. *207* (GH) *H.*
Lebrun, J. *789* (GH, US) Cr.
Lynes, H. *596* (US) *Ca.*
Mearns, E. A. *1011* (US) *Cr; 1377* (GH, US) *Cr; 2403* (US) *Cr.*
Quer, Font. *121* (UC) *H.*
Schimper, W. *276* (UC, US) *Ca; 359* (MO) *Ca; 1077* (MO, US) *Ca; 1513* (GH, MO) *Ca; 1535* (GH, MO, US) *Ca.*
Warion, A. *1360* (MO) *H.*

Oceania.—

Degener & Topping. *17896* (MO) *Cr.*
Fosberg, F. R. *13348* (MO) *D; 13830* (MO) *D; 24390* (X) *D; 26503* (X) *D; 26935* (X) *D.*
Seemann, B. *367* (GH) *Cr.*
White, C. T. *10762* (GH) *H.*

Explanation of Plate

PLATE 10

A, Xochihuauhtli (Sahagún, ca. 1570a, 5:137).

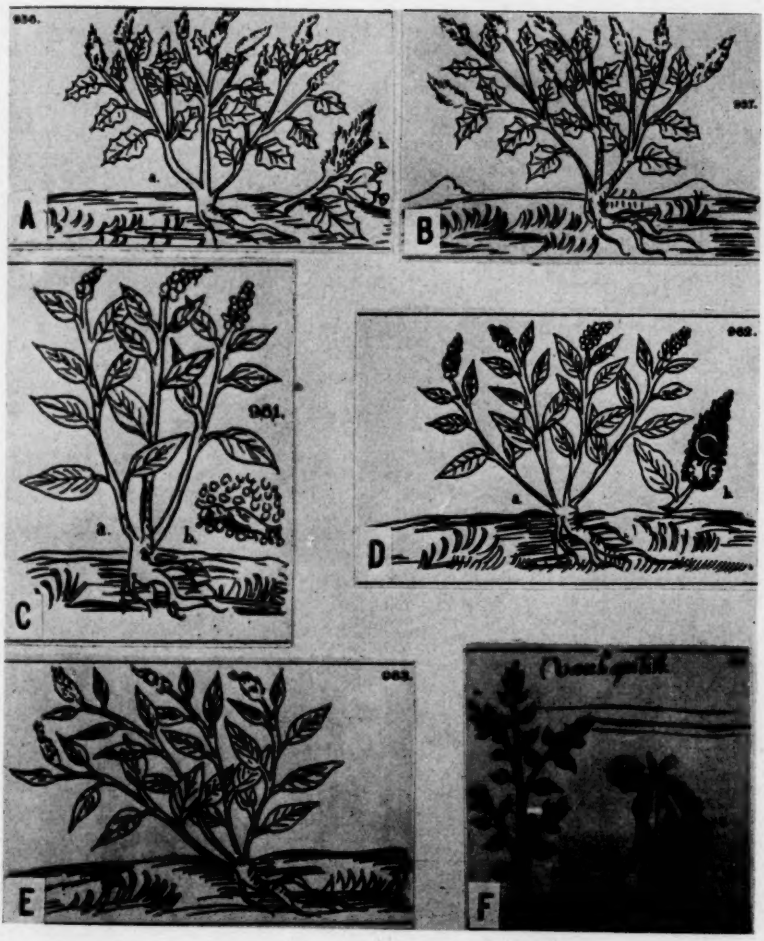
B, Tlapalhuauhtli (Sahagún, *ibid.* 137).

C, Michihuauhtli (Sahagún, *ibid.* 138).

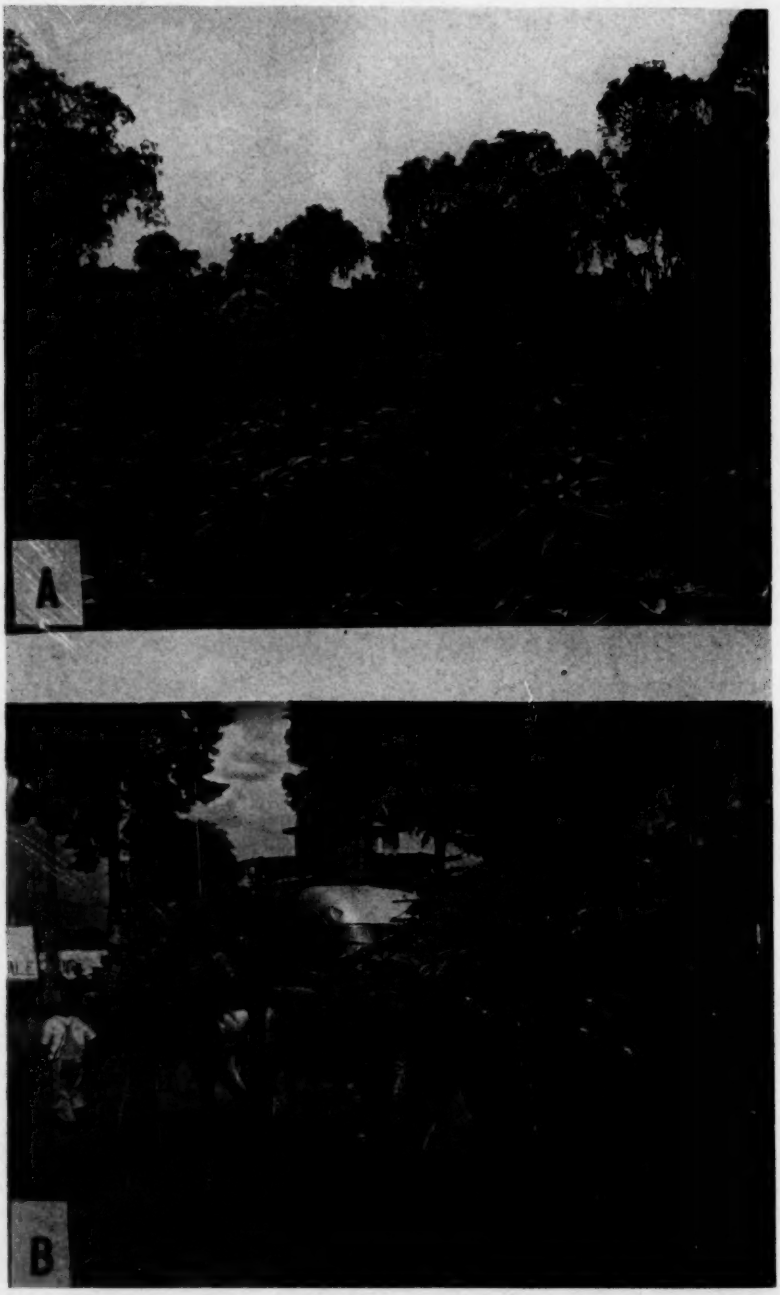
D, Tezcahuauhtli (Sahagún, *ibid.* 138).

E, Petzícatl (Sahagún, *ibid.* 138).

F, Huauhquilitl (Sahagún, *ibid.* 102).



SAUER—GRAIN AMARANTHS



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Explanation of Plate

PLATE 11

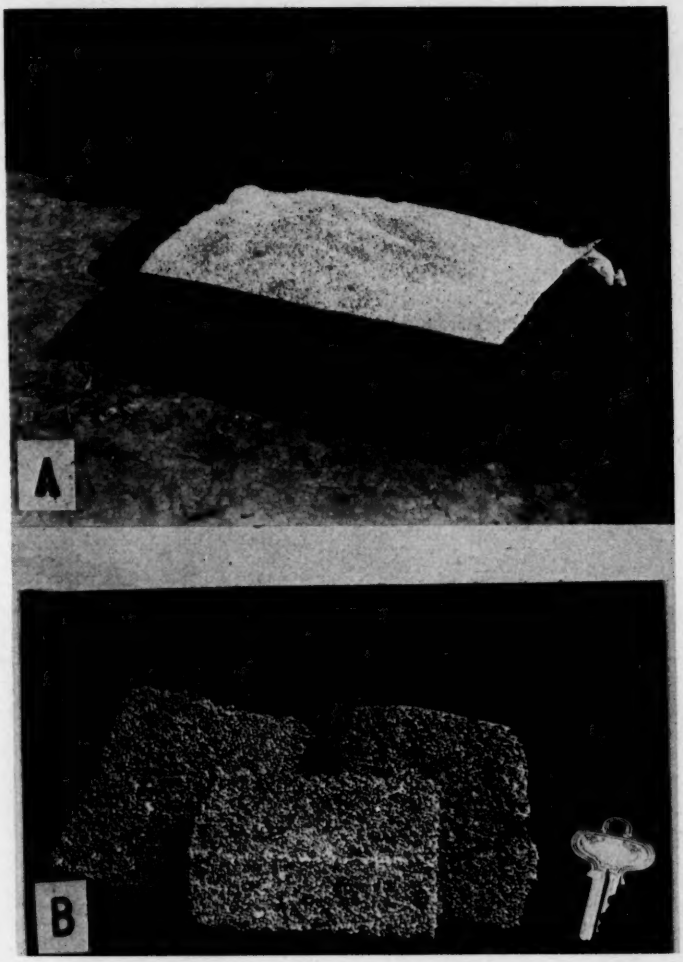
A, Young grain amaranths near San Gregorio Atlapulco, D. F.

B, Transporting harvested amaranths, Tulyehualco, D. F.

Explanation of Plate

PLATE 12

A, Popped amaranth seed prepared for *niguas*, San Martín Jilotepeque, Chimaltenango. B, *Niguas* made at San Juan Sacatepéquez, Guatemala.



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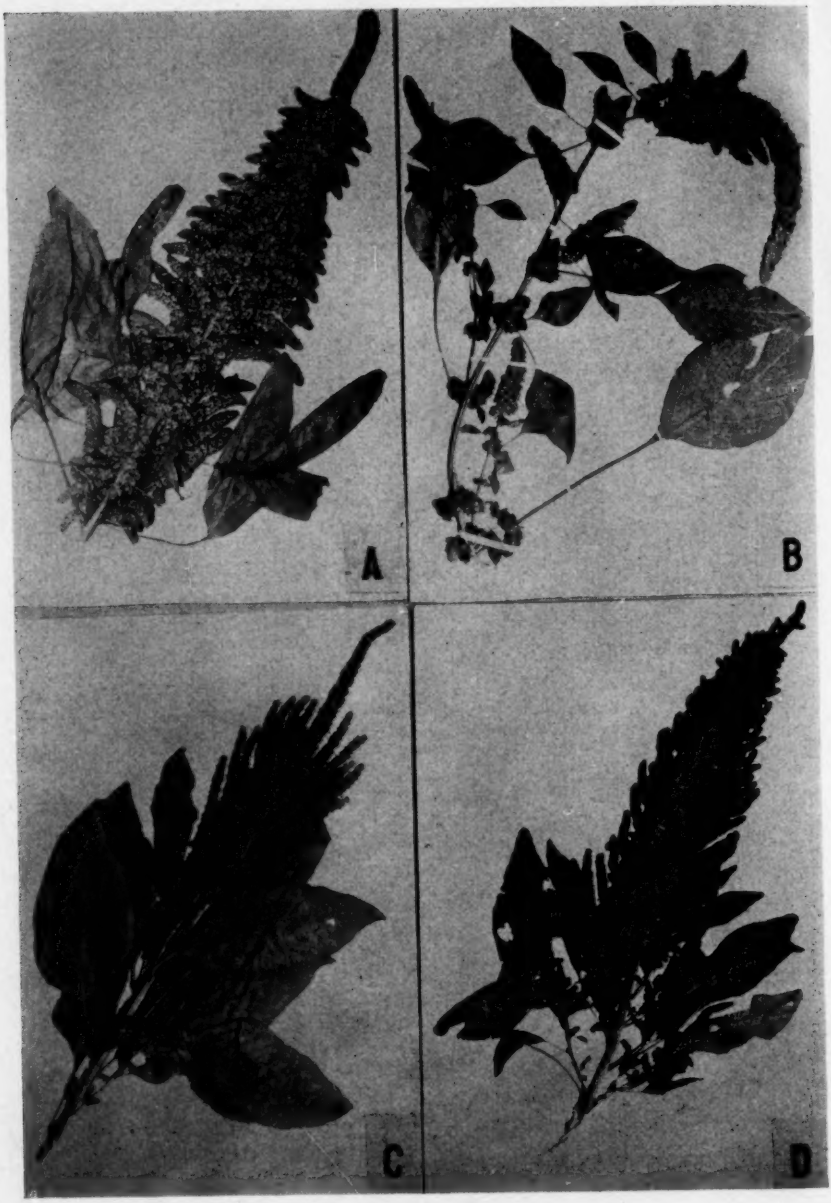


SAUER—GRAIN AMARANTHS

Explanation of Plate

PLATE 13

A, Inflorescence of *A. leucocarpus*, common race, × ¼. (Specimen: *J. D. Sauer 1162-E*).

B, Inflorescence of *A. leucocarpus*, Arizona race, × ¼. (Specimen: *J. W. Powell s. n.*, type of the species).

C, Inflorescence of *A. leucocarpus*, aberrant race, × ¼. (Specimen: *J. D. Sauer 1355-B*).

D, Inflorescence of *A. cruentus*, common race, × ¼. (Specimen: *J. D. Sauer 1240-B*).

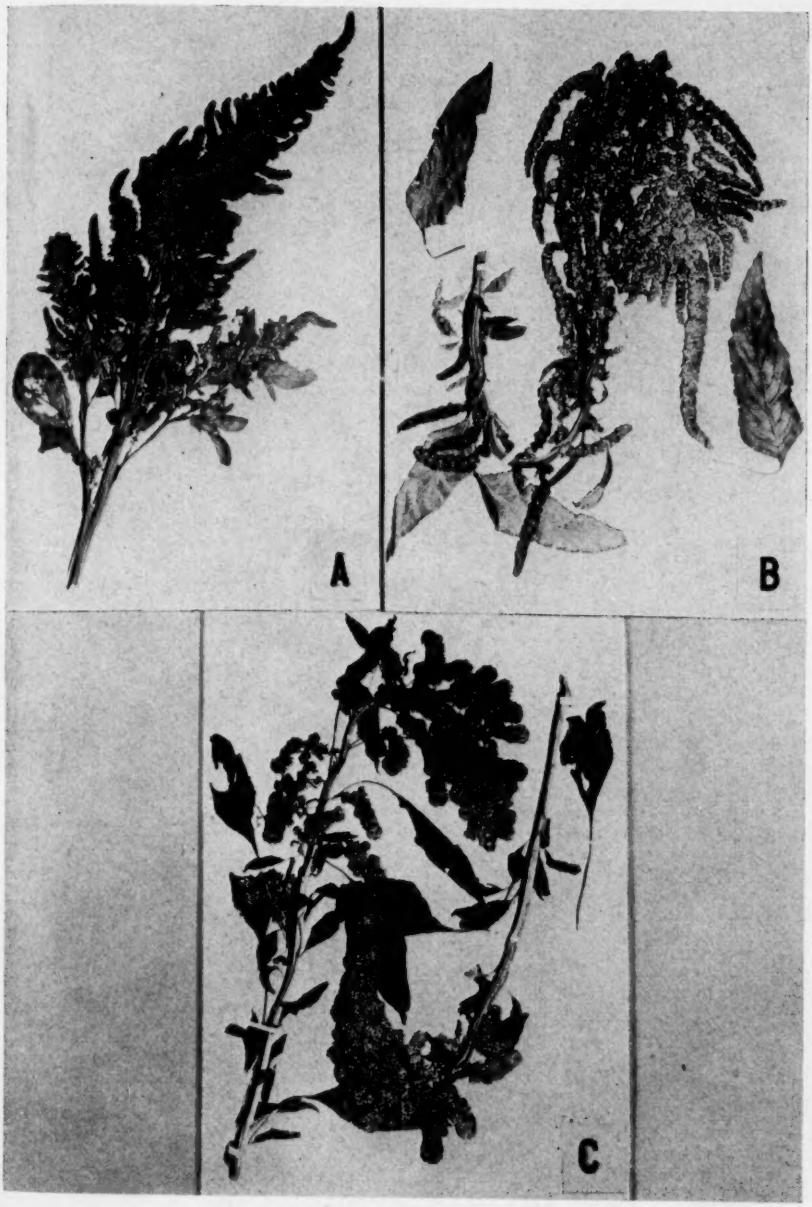
Explanation of Plate

PLATE 14

A, Inflorescence of *A. cruentus*, Mexican race, × ¼. (Specimen: *J. D. Sauer 1266-A*).

B, Inflorescence of *A. caudatus*, ×¼. (Specimen: *M. Cárdenas 3513*).

C, Inflorescence of *A. edulis*, × ¼. (Specimen: *A. T. Hunziker 2127*).



SAUER—GRAIN AMARANTHS

Appendix

EXTRACTS FROM EARLY LATIN AMERICAN SOURCES

(Figures in parentheses refer to pagination of editions cited in List of Sources.)

A. ANONYMOUS, CA. 1540.—

(20). Iba esta diosa [Cueravaperi] dos fiestas con sus sacerdotes á la ciudad de Mechuacan por la fiesta de Cuingo y Corindaro . . . Era tenida en mucho en toda esta provincia, y nombrada en todas sus fabulas y oraciones, y decían que era madre de todos los dioses de la tierra, y que ella los envió â morar á las tierras, dándoles mieses y semillas que trujesen.

(108). Luego como vieron los indios los españoles, de ver gente tan estraña y ver que no comían sus comidas de ellos, y que no se emborrachaban como ellos, llamábanlos tucupacha, que son dioses . . . y á los caballos llamaban venados, y otros tuycen, que eran unos como caballos que ellos hacían en una su fiesta de Cuingo, de pan de bledos.

B. ANONYMOUS, CA. 1550.—

Cap. 1 (128). Las mozas deste recogimiento, dos días antes de la fiesta deste ídolo, Huitzilopuchtli, molían mucha cantidad de semilla de bledos juntamente con maíz tostado, y después de molido, amasábanlo con miel, y hazían de aquella masa un ídolo tan grande como era el de madera . . . Hecho esto, salían todas las doncellas con el aderezo referido y sacaban de su recogimiento unos trozos de massa de maíz tostado, y bledos que es la mesma de que el ídolo era hecho, hechos á manera de huevos grandes, y entregábanlos á los mancebos, y ellos subíanlos arriba, y poníanlos á los pies del ídolo por todo aquel lugar hasta que no cabían mas: á estos trozos de masa llamaban los huessos y carne de Huitzilopuchtli.

C. SAHAGUN, CA. 1570b.—

Libro 1, Cap 13 (1:30). A este dios [Xiuhtecutli] se le hacía fiesta cada año, al fin del mes que se llama izcalli . . . y ofrecíanle unos pastelejos que llaman quiltamalli, hechos de bledos, y estos mismos comían por su honra.

Libro 1, Cap. 14 (1:32–34). A la honra de este dios [Xochipilli] hacían fiesta, y su fiesta se llamaba xochilhuitl, la cual se contaba entre las fiestas movibles . . . Ofrecían asi mismo dos pasteles que llaman tzoalli . . . y el uno de estos pastelejos era negro y el otro bermejo. La otra gente ofrecía diversas cosas: unos ofrecían maíz tostado, otros maîz tostado revuelto con miel y con harina de semilla de bledos . . . otros ofrecían unas tortas hechas de semillas de bledos.

Libro 1, Cap. 15 (1:36). Cuando hacían fiesta a este dios [Omacatl], que era de noche, comulgaban con su cuerpo; y para esta comunión los principales y teopixques, y los que tenían cargo de los barrios, hacían de massa una figura de un hueso grueso . . . Hecho esto, repartían aquella figura de hueso que habían hecho de masa que se llama tzoalli, y dividíanla entre sí, y comían cada uno lo que le cabía.

Libro 1, Cap. 21 (1:48–49). Todos los montes eminentes, especialmente donde se arman nublados para llover, imaginaban que eran dioses . . . El que había hecho voto á alguno ó á algunos montes ó de estos dioses hacía su figura de una masa que se llama tzoalli, y poníalos en figura de personas; no lo hacía él por su manos, porque no le era lícito, sino rogaba á los sátrapas, que eran en esto experimentados y para esto señalados, que le hiciesen estas imágenes á quien había hecho voto.

Libro 2, Cap. 4 (1:89–90). Al cuarto mes llamaban uey tozoztli . . . Todas las muchachas llevaban á cuestas mazorcas de maíz del año pasado, é iban en procesión á la diosa Chicomecôatl, y tornábanlas otra vez á su casa como cosa bendita, y de allí tomaban la semilla para sembrar el año venidero . . . Hacían de masa que llaman tzoalli la imagen de esta diosa, en el patio de su cu, y delante de ella ofrecían todo género de maíz y todo género de frijoles, y todo género de chía, porque decían que ella era la autora y dadora de aquellas cosas que son mantenimientos para vivir la gente.

Libro 2, Cap. 10 (1:97–99). Al décimo mes llamaban xócotl huetzi . . . En lo alto del arbol estaba en pie la imagen de aquel dios [Xiuhtecutli] hecha de masa que llaman tzoalli.

Libro 2, Cap. 13 (1:102). Al décimo tercero mes llamaban tepeilhuitl. En este mes hacían fiesta á honra de los montes eminentes . . . hacían las imágenes en figura humana â cada uno de ellos, de la masa que se llama tzoalli, y ofrecían delante de estas imágenes en respeto de estos mismos montes. Hacían á honra de los montes unas culebras de palo ó de raíces de árboles, y labrâbanles la cabeza como culebra; hacían también unos trozos de palo gruesos como la muñeca, largos, llamábanlos ecatonti; así á estos como à las culebras los investían con aquella masa que llaman tzoal.

Libro 2, Cap. 16 (1:107). Al décimo sexto mes llamaban atemoztli. En este mes hacían fiesta á los dioses de la pluvia . . . Hacían las imágenes de los montes de tzoal.

Libro 2, Cap. 18 (1:109–110). Al mes décimo octavo llamaban izcalli. En este mes hacían fiesta al dios del fuego que llamaban Xiuhtecutli . . . Un tamal hecho de bledos, que ellos llamaban uahquiltamalli, los cuales todo el pueblo ofrecía aquel día y todos comían de ellos por honra de la fiesta.

Libro 2, Cap. 24 (1:134–137). Al quinto mes llamaban tóxcatl . . . Hacían de masa que se llama tzoalli la imagen de Huitzilopochtli, tan alta como un hombre hasta la cinta.

Libro 2, Cap. 29 (1:169–170). Al décimo mes llamaban xócotl huetzi . . . Componían de papeles á una estatua, como de hombre, hecha de masa de semillas be bledos . . . Ponían también tres tamales grandes hechos de semillas de bledos sobre la cabeza de la imagen, hincados en tres palos.

Libro 2, Cap. 32 (1:185). Al décimo tercero mes llamaban tepeilhuitl. En la fiesta que se hacía en este mes cubrían de masa de bledos unos palos, que tenían hechos como culebras, y hacían unas imágenes de montes fundadas sobre unos palos hechos á manera de niños, que llamaban hecatonti; era de masa de bledos la imagen del monte, poníanle delante junto unas masas rollizas y larguillas de masa de bledos á manera de bezos, y estos llamaban yomio. Hacían estas imágenes á honra de los montes altos . . . y hacían unas tortillas pequeñuelas de masa de bledos amarillos.

Libro 2, Cap. 34 (1:192–198). Al décimo quinto mes llamaban panquetzaliztli . . . La estatua de Huitzilopochtli era hecho de masa de bledos.

Libro 2, Cap. 35 (1:200–201). Al mes décimo sexto llamaban atemoztli . . . Componían las imágenes que estaban hechas de masa de bledos, algunos tenían hechas cinco, algunos diez y otros quince: eran las imágenes de los montes.

Libro 2, Cap. 37–38 (1:206–213). Al décimo octavo mes llaman izcalli . . . Las mujeres, toda la gente se ocupaba en hacer unos tamales que llaman huauhquiltamalli, y también en amaneciendo los iban á ofrecer delante de estatua, y así estaba gran cantidad de ellos delante la estatua . . . También ofrecían al fuego cada uno en su casa cinco huauhquiltamalli, puestos en un plato, y también ofrecían sobre las sepulturas de los muertos, adonde estaban enterrados, á cada uno un tamal.

Apendice del Libro 2 (1:215). Tres fiestas se hacían cada año a Huitzilopochtli entre los mexicanos. La una de ellas se hacía en el mes que se llama panquetzaliztli. En esta fiesta á él y á otro que se llamaba Tlacauépan Cuexcótzin, los subían á lo alto del cu, y es que hacían sus imágenes de tzoalli, grandes como una persona . . . Cocían primero la masa y despues formaban de ella las estatuas, en toda una noche.

Libro 3, Cap. 1 (1:262). El día cuando amasaba y hacía el cuerpo de Huitzilopochtli para celebrar la fiesta que se llamaba panquetzaliztli, tomaban semillas de bledos y las limpiaban muy bien, quitando las pajas y apartando otras semillas que se llamaban petzicatl y tezcahuauhtli, y las molían delicadamente, y despues de haberlas molido, estando la harina muy sutil, amasábanla de que se hacía el cuerpo de Huitzilopochtli . . . luego deshacían y desbarataban el cuerpo de Huitzilopochtli, que era de una masa hecha de semilla de bledos, y el corazón de Huitzilopochtli, tomaban para el señor ó rey, y todo el cuerpo y pedazos que eran como huesos del dicho Huitzilopochtli lo repartían en dos partes, entre los naturales de México y Tlatilulco.

Libro 7, Cap. 9 (2:267–268). Antes que llegase ce tochtli, á quien temían mucho por el hambre, todos procuraban de juntar y esconder en sus casas muchos mantenimientos, y todos los géneros de semillas que se pudiesen comer, aunque eran comidas muy bajas, cuales son las que se dicen en este capítulo . . . huauhtli polocayo es la semilla de los cenizos sin limpiar, con todas sus inmundicias.

Libro 7, Cap. 13 (2:273). De la dicha manera hecha la lumbre nueva, luego los vecinos de cada pueblo, en cada casa . . . comían tzouatl, que es comida hecha de bledos con miel, y mandaban a todos ayunar y que nadie bebiese agua hasta medio día.

Libro 9, Cap. 14 (2:380–381). Cuando habían de matar á los esclavos . . . los llevaban al templo de Huitzilopochtli . . . y al tiempo de la media noche . . . apagaban el fuego, y á oscuras daban de comer á los esclavos unas sopas de una masa que se llama tzoalli, mojadas con miel, á cada uno de ellos cuatro bocados.

Libro 10, Cap. 29 (3:127–135). Estos dichos quaquatas, como en su tierra de ellos, es en el valle que llaman Matlatzinco, hace grandísimo frío . . . solamente se da maíz y frijoles, y unas semillas que son de mantenimiento que se llaman huauhtli . . . En su tierra [Michoacán] se dan muy bien los bastimentos, maíz, frijoles, pepitas, y fruta y las semillas de mantenimientos llamadas huauhtli.

Libro 11, Cap. 7 (3:233–234). Una de las hierbas que se comen cocidas se llama huauhquilitl, que son bledos; es muy verde, tiene las ramas delgadillas y altillas, tiene las hojas anchuelas. Los tallos de esta hierba se llaman huauhtli, la semilla se llama de la misma manera; esta hierba se cuece para comer, sabe á cenizos, exprímese del agua en que se cuece para comerse; hácense tamales de esta hierba, los cuales se llaman quiltamalli; hácense tortillas. Es hierba muy comun y comenla mucho; es como cenizos de España. Otra hierba se come cocida llámase quiltonilli; tiene las hojas anchuelas cuando es pequeña. Este hierba es comestible, y cuando ya es grande llamase petzícatl; cuécese con salitre; exprímese del agua para comerla. Esta hierba cría una semilla negra que se llama pítzitl.

D. *HERNÁNDEZ, CA. 1575c.—*

Liber 6, Cap. 44 (2:129–131). Paratur quoque Michuauhatolli, id est Atolli sementiferum ex Michihoauhtli torrefacto hoc semine, et redacto in laevorem cumque exposcit occasio, in aquam conjecto, ea mensura, quae nullam adferat spissitudinem, et densitatem, et insperso melle Metl cocto . . . Est et Hoauhatolli, quod ex Blitis rubeis fit, ingeriturque insperso melle; praeterea Michihoauhatolli, quod ex Michihoauhtli paratur, pisturato nempe Blitorum genere, quod symphoniam a varietate coloris quidam vocant.

Liber 9, Cap. 64 (2:340–341). Reperias in hac Nova Hispania plura Atriplicis agrestis genera, quae universim Hoauhtli, seu Hoauhquilitl vocare Mexicenses consueverunt, et in hortis suis, atque viridariis magna cura serere, atque excolore, qualia sunt Tlapalhoaquilitl, seu Tlapalhoauhtli, radice crassa, brevi, et fibrata, unde prodeunt caules rubei, et in eis folia ejusdem coloris, oblonga, et serrata per intervalla, quae elixa eduntur, suntque adeo grati saporis . . . Praeterea Nexhoauhtli viridis tota, edulisque, et Chichichoauhtli, quae ob amaritudinem locum non habet inter olera, foliis e viridi purpurascentibus, et coccineis floribus, et alia permulta, quorum nec usus est, nec rationem ullam habendam duxi, pro olere magna ex parte eduntur elixa . . . Parant Mexicani e duorum primorum generum semine globulos, ac potionum Michihoauatolli vocatam, qua utuntur velut gratissimo cibo.

E. DURÁN, CA. 1580.—

Cap. 80 (2:85–90). Un ydollo de Huitzilopochtly . . . de una massa que llaman tzvally la qual se hace de semilla de bledos y maiz amassado con miel . . . Las moças del recoximiento de este tenplo dos dias antes de la fiesta de este ydolo de que bamos tratando molian mucha cantidad de la semilla de bledos quellos llaman huauhtly juntamente con maiz tostado despues de molido amasavanlo con miel negra de los magueies despues de amassado hacian un ydolo de aquella massa tal y tan grande como era el de palo . . . tzoalli con miel era la massa de aquel ydolo.

Cap. 90 (2:166). Fiesta de Xocotlhuetzi dios particular de los tecpaneca que son los de Coyoacan . . . el día de su fiesta hacian vn pajaro de massa de simiente de bledos que hemos llamado tzoally la qual massa perpetuamente siruio a estos para efigie de ydolos y carne y guessos de los diosses suyos para despues comerse aquella massa.

Cap. 96 (2:204). La fiesta . . . se llamaba Tepeylhuitl que quiere decir fiesta de cerros . . . Toda la multitud de la gente que en la tierra había se ocupaba en moler semilla de bledos y maiz y de aquella masa hacer un cerro que representaba el volcan al cual ponían sus ojos y su boca y le ponían en un preminente lugar de la casa y alrededor de él ponían otros muchos cerrillos de la misma masa de tzoalli . . . Sacrificaban esta masa que habían representado los cerros donde despues de hecha la ceremonia se la comian con mucha reverencia. Este día los sacerdotes buscaban en el monte las mas tuertas y corcobadas ramas que hallaban y llevabanlas al templo y cubríanlas con esta masa.

F. GROUP OF RELACIONES, CA. 1580.—

Castañeda, 1580 (218–236). Aculma: Coxen mayz e frisoles e chian e guautli, de que se sustentan. San Juan Teutihuacán: Cogese mucho mais en el dicho pueblo y sus terminos, y frisoles, y guautle y chia para su sustento . . . Tequizistlán: Las semyllas que se sienbran son mayz, chian y huautly . . . Tepexpa: Los mantenimyentos de que sienpre an vsado y vsan son los comunes entre ellos: mayz y frisoles y calabazas y huautli . . . cojen los naturales para sus sustento mayz y frisoles y clabazas y axin y chian y guauhtli.

Castañeda, 1581 (227). Guauhtla: Tienen semillas de mayz, frisoles, calabaças, huauhtli . . .

Contreras Figueroa, 1580 (16–37). Axacupan: Thenyan para su sustento lo que agora tienen, que es pan de mahiz y semylla de bledos . . . los granos y semyllas desta tierra que le sirve de sustento son mahiz, frisoles, agi, chian, guautle, que es semylla de bledos . . . Yetecomac: Las semillas que entre ellos se tienen y se vsan son mahiz, frisoles, chian, guautle, que es semilla de bledos, y de esta semylla se haze vn pan a su modo . . . Tornacustla: Comyan pan de mahiz, frisoles, chian, guautle . . . Tecpatepec: Tienen mahiz, frisol, chian, huautle . . .

Godínez Maldonado, 1581 (287). Tetela del Volcán y Gueyapa: Lo que alli se a cojido y coje es maiz en abundançia, frisol, chia, vautli . . .

González, 1581 (130). Xonotla: Los granos y semyllas que tienen son chian y guahtli . . .

Moniaraz Zamorano, 1581 (310). Quauhquilpan: Se siembra y coge mahiz, avnque poco por la esterilidad de la tierra, y frisoles, y la semilla del huauhtli, que es como grano de mostaza de que se mantienen los yndios.

Pinto, 1579 (p. 92). Iscateupa: Las semyllas de que se aprobechan son frisoles, chian, chile, maiz, pepitas, quilites: destos se aprovechan agora y dicen que siempre antiguamente tubieron estas semyllas.

Pomar, 1582 (p. 49–58). Tezcoco: Los mantenimientos de que antes usaban es de lo propio que al presente usan y se mantienen, que es lo principal el maíz . . . y de huauhtli, y de michihuauhtli . . . el huauhtli, que es una semilla como de nabos, y de su propia color, salvo que es chatilla como lantejas, de que después de molido y amasado hacven unos bollos metidos en hojas de maíz, que cuecen en ollas, ó haciéndola tortillas cocidas en un comal . . . tienen michhuauhtli, que es otra semilla blanca y más menuda: de este hacen bollos por la propia orden que se ha dicho del huauhtli, y de esta suelen beber después de tostada y molida y deshecha en agua miel.

Vera, 1581 (68). Chila: Se da maiz, chile, frisoles, pepitas, chia y guautli.

G. TEZOZOMOC, CA. 1598.—

Cap. 1 (8). Y al tiempo que llegaron á esta ciudad [Tenochtitlán] habían andado y caminado muchas tierras, montes, lagunas, y ríos . . . La comida que traían era maíz, frijol, calabaza, chile, jitomate y miltomate, que iban sembrando y cogiendo en los tiempos y partes que descansaban y hacían asiento, como dicho es, y como liviano que era el chian y huauhtli lo traían cargado los muchachos.

Cap. 3 (15). Allí en Xaltocan hicieron camellones dentro del lago Chinamitl, sembraron maíz, huautli, frijol, calabaza, chilchotl, jitomate.

Cap. 15 (56). Subidos los tecpanecas en un alto de un monte que llaman Axochco, desde allí comienzan á vocear los tecpanecas, diciendo: señores míos, mexicanos, no haya mas, habed clemencia y piedad de nosotros, sosieguen vuestras armas, y reposen vuestras personas . . . os daremos frijol, pepita, huauhtli, chian para vuestro sustento, y maíz por todos los tiempos de los años.

Cap. 48 (209). Llevároníe luego á Toluca á descansar, y en este ínter sobrevino Chimalteuctli, señor de los matlazincas, y díjoles: Señores mexicanos, cese ya vuestro orgullo y braveza, que ya os somos vuestros vasallos y tributarios: mirad, señores, que en esta tierra y pueblo no hay otra cosa sino maíz, frijol, huauhtli, chian, y tea para alumbrar de noche, que es candela, y esteras, petlatl. Esto es, señor, lo que en este pueblo vuestro se dá y cría, y no otra cosa.

Cap. 74 (353). Llegados á Teloloapan partieron la gente en tres partes igualmente, y de las casas que había hechas y habían sido de los muertos, las mejores tomaron los mexicanos; y asimismo los pueblos cercanos á ellos mandaron llevasen maíz, frijol, huauhtli . . .

H. RUÍZ DE ALARCON, 1629.—

Cap. 3 (137–138). Donde mas manifiestamente ay formal ydolotria, es al fin de las aguas, con las primicias de una semilla menuda mas que mostaça, que llaman huauhtli, porque tambien el demonio quiere que le ofrescan primicias: es pues esta semilla mas temprana, endurece y sasonarse qu otra ninguna, y assi la cojen quando el mayz que llaman temprano o nemesina empieça a espigar, que en tierras calientes suscede en dos messes: desta semilla hazen vna beuida como poleadas para beuerla fria, y hazen tambien vnos bollos, que en la lengua llaman tzoalli, y estos comen cossidos al modo de sus tortillas. La ydolatria esta en que accion de gracias de que se aya saçonado, de lo primero que coxen bien molido y amasado, hazen vnos ydolos de figura humana de tamaño de vna quarta de vara poco mas o menos . . . repartiendo los idolillos a pedaços como por reliquias se los comen entre todos.

I. COBO, 1653.—

Libro 4, Cap. 2 (1:337). Hállanse así mismo las yerbas siguientes: Bledos blancos y rojos, y son comida muy ordinaria de los indios, y en la ciudad de Guamanga se hacen de la semilla de los Bledos blancos muy regalados turrones con azúcar.

Libro 4, Cap. 5 (1:350). La Quinua es una planta muy parecida á los bledos.

J. SERNA, 1656.—

Cap. 2 (288–289). Hállase por confessiones de algunos delinquentes, que auía en algunos Pueblos de el Valle algunos viejos, que tenían por officio el sacar el fuego nuevo, que era, segun estoy informado, que este tal Ministro del Demonio, ó sacaba el fuego con vnos palillos, ó lo traían de la vezindad con los poquietes, y allí le offrescian vnos tamalillos de Zoales, que es vna semilla de Bledos, los quales offrescian al fuego, echandolos por las quatro partes de la casa . . . por declaración de vn indio de Cumpahuacan, de donde se tuvo noticia y originó esta complicidad.

K. ANONYMOUS, CA. 1760.—

(31). Otra semilla siembran solos los Jovas, y llaman coguet, ex Mexicani zoale. Es como semilla de quelites, de color amarillo. Su primera cosecha son las ojas de la mata; y la segunda dicha semilla; pero para comerla, la benefician de esta suerte: en una canastita hecha de palma, hechan un almud, ó lo que quieren de dicha semilla, van al Rio, y dentro de el agua lo estan pisando con un pie hasta que rrebienta el grano; y mientras lo pisan, está hechando mucha espuma. Despues lo tuestan, y muelen; y así rebuelto con agua fria, lo comen; y es un refresco tal de bueno.

L. ANONYMOUS, 1777.—

Fascicles 261–274. Por Agosto tambien, pero solo en barrancas templadas, siembran una simiente, que en la Nueva España nombran alegría, y los tarahumares nombran oguigui. Es á manera de ajonjolí aunque mas menuda y redonda, tostada revienta y crece mucho, y es de mui buen gusto, se cosecha por Noviembre . . . De la alegría tostada, ó comen seca, ó la hacen bebida moliéndola con agua . . . Delas ojas delos bledos (que naturalmente tambien nacen muchos) comen los indios crudas, ó cocidas, y tambien hacen bebida molidas con agua, ó solas, ó revolviéndoles maíz tostado . . . De las semillas delos dichos bledos que son de dos maneras, blanco y encarnado, y al blanco llaman temevali, y al encarnado chullaca, hacen pan, ó comen tostada, ó hacen bebida.

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